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THE UNIVERSITY OF KANSAS
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VOL. XLIV] SEPTEMBER 13, 1963 [NO. 1

Hybridization Among Three Species of *Ratibida*

BY

S. WESLEY JACKSON

ABSTRACT: The origin of *Ratibida* and its relationship to *Dracopsis*, *Rudbeckia*, and *Echinacea* have been discussed. It has been suggested that the basic chromosome number and ancestral karyotype of *Ratibida* is represented in *R. tagetes*. Meiotic studies of *R. tagetes* × *R. columnaris* indicate the lower chromosome number in *R. columnaris* may have been derived from unequal reciprocal translocations, resulting in a small chromosome with relatively inert genic material which then became lost. Further translocations and inversions have occurred since the isolation of the two species, resulting in very low pollen fertility in the F_1 hybrid. Pollen fertility of 50.5 to 75.7 percent in F_1 plants with normal-appearing meiotic stages beginning with diplotene has been attributed to "cryptic structural hybridity" in either *R. columnaris* or *R. peduncularis* var. *picta* or both.

Studies of meiosis, karyotypes, and morphology show *R. columnaris* and *R. peduncularis* var. *picta* to be more closely related than *R. columnaris* and *R. tagetes*.

INTRODUCTION

Ratibida Raf. is an epappose genus of the family Compositae, tribe Heliantheae. The genus, consisting of five species, has a wide range in North America. Morphologically it is closely related to *Rudbeckia*, *Dracopsis*, and *Echinacea*.

During this study, artificial hybrids were obtained between *Ratibida columnaris* (Sims) D. Don and *Ratibida tagetes* (James) Barnh., and between *R. columnaris* and *Ratibida peduncularis* (T. & G.) Barnh. var. *picta* (Gray) Sharp. Thus far, crosses of these three species to *Ratibida pinnata* (Vent.) Barnh. have been unsuccessful. The cross between *R. tagetes* and *R. peduncularis* var. *picta* has not been verified yet, and *Ratibida mexicana* (Wats.) Sharp was not available for experimental study.

Studies of meiosis have been utilized to determine the chromosomal alteration that has taken place during the isolation of the species and to gain an idea of the relative fertility of the hybrids. The latter is of importance in assessing the possbilities of introgression among the various species.

An attempt has been made to obtain morphological and cytological data to show the relationship of three species within the genus.

ACKNOWLEDGEMENTS

The writer wishes to express his appreciation to Dr. R. C. Jackson and Dr. R. L. McGregor for their advice and co-operation throughout this study. He is indebted to Dr. R. H. Thompson for his criticisms and valued suggestions pertaining to the writing of the manuscript. Acknowledgement is also due the staff and graduate students of the Department of Botany, University of Kansas, who furnished materials and advice on problems in preparation of the manuscript. During this study specimens were examined from the herbaria of the University of Kansas, the University of Texas, and the University of New Mexico. The writer expresses his appreciation to the curators of these herbaria for making specimens available for study.

MATERIALS AND METHODS

Herbarium studies: Herbarium material of the five species of the genus was obtained from three different herbaria. The specimens were examined to determine the distribution and the variation in the genus.

Collections: Specimens of the species and artificial hybrids are deposited in the Herbarium of the University of Kansas.

Various ligule color patterns of *R. columnaris* and *R. peduncularis* var. *picta,* and yellow-liguled plants of *R. pinnata* and *R. tagetes* were collected in the field and transplanted to the greenhouse and experimental garden by Mr. Leon Richards. Seed representing various populations were also collected in the field and grown in the greenhouse. Table 1 gives the collection data of the plants studied.

Germination: Achenes were germinated in Petri dishes containing two pieces of damp filter paper. Rubber bands one and one-half inches wide were placed around the dishes to prevent drying. Seedlings were either fixed for cytological study or transferred to pots in the greenhouse.

Crossing: All crossing was done in the greenhouse. The heads were bagged before anthesis of the disc flowers to prevent pollen contamination. Because the four species involved in the study are self sterile, heads of any two plants involved in a cross were rubbed together daily until flowering was finished. The bags were left on the plants until the achenes had matured and were harvested, seven to nine weeks after the ligules had opened.

TABLE 1.—Collection Data.

CODE NUMBER	Species	Locality
64	*E. columnaris f. columnaris*	Quay Co., N. Mexico 14.4 mi. E. of San Jon.
99	*R. columnaris f. columnaris*	Barber Co., Kansas S. of Sun City
118	*R. columnaris f. columnaris*	Barber Co., Kansas S. of Sun City
31	*R. columnaris f. pulcherrima*	Otero Co., N. Mexico near Cloudcroft
65	*R. columnaris f. pulcherrima*	Otero Co., N. Mexico near Cloudcroft
137	*R. columnaris f. pulcherrima*	Otero Co., N. Mexico near Cloudcroft
19	*R. peduncularis* var. *picta*	Wilson Co., Texas 0.7 mi. S. of Stockdale
26	*R. peduncularis* var. *picta*	Wilson Co., Texas 5.3 mi. N. of Stockdale
27	*R. peduncularis* var. *picta*	Wilson Co., Texas 5.3 mi. N. of Stockdale
72	*R. peduncularis* var. *picta*	Guadalupe Co., Texas 11.4 mi. S. of Seguin
153	*R. peduncularis* var. *picta*	Guadalupe Co., Texas 11.4 mi. S. of Seguin
29	*R. tagetes*	Bernalillo Co., N. Mexico

Fixation: The following fixatives were used for the cytological material: (1) six parts of 100 percent alcohol, three parts of chloroform, and one part of propionic acid; (2) two and one-half parts of 100 percent alcohol, one-half part of chloroform, and one part of propionic acid; (3) two parts of 100 percent alcohol, one part chloroform, and one part propionic acid. Minimum time for fixation was 48 hours.

Cytological material for meiotic study was fixed between 11:00 a. m. and 12:00 noon.

Staining: The propioniocarmine squash technique was used for staining meiotic chromosomes. Difficulty was experienced in obtaining good preparation of the parental species and hybrids since the chromosomes tended to stick together when taken directly from

the fixative. Chromosomes of the material were not so sticky when the fixative had been replaced with 75 to 85 percent alcohol for at least seven days.

Pollen grains were stained in lactophenol-cotton blue for at least 24 hours before examination. Grains staining a uniform blue were counted as viable, and those which stained only partially or not at all were counted as inviable.

Preparation of figures: Drawings of meiotic phases were made at a magnification of approximately × 1425. All figures were mounted on plates, photographed, and reduced to page size. Magnification of the figures on the same plate are relative only to the reduction of that plate.

DISTRIBUTION AND MORPHOLOGICAL VARIATION OF THE GENUS

Ratibida is confined to North America but has a wide distribution within that area. According to Sharp (1935), the center of distribution is in Kansas and Nebraska.

Ratibida columnaris covers the widest geographic range, being found in valleys, on prairies, plains, and high mountain areas from Saskatchewan in Canada to central Mexico. Over this wide range one finds considerable variation in the species. Plants from southwestern Kansas may be short and bushy with deeply dissected leaves and rather small heads containing very small flowers. On the other hand, plants from the mountain areas of Montana, New Mexico, and Mexico have a taller, more robust appearance and large flowers. Achenes from Barber County, Kansas, and Otero County, New Mexico, were planted in the greenhouse under reasonably similar growing conditions, and the cultured plants of the two areas retained the general morphology of their respective parents.

Yellow and purple pigment combinations in the ligules are found throughout the range of the species. However, the pattern may have been different at one time because in some areas purple is more prevalent than in others.

R. columnaris is weedy by nature, occupying an area abundantly one year but being absent two or three years later. Because of this weedy nature, mobility, and genetic diversity (expressed in considerable morphological variation), *R. columnaris* lends itself quite well to speciation. Its distribution overlaps at least three other species of the genus.

Ratibida tagetes is confined largely to the Southwest, rarely extending north of the 40 degree parallel. It extends south to Texas and Northern Mexico (Sharp 1935) where it occurs chiefly in the dry plains and prairies, apparently able to withstand dry conditions better than the other species of the genus.

Ratibida peduncularis, a vigorous, robust species, is confined to the Coastal Region of Texas and Louisiana, apparently favoring a more humid climate. This species has the most limited range of the genus.

Ratibida pinnata is the eastern-most species and, according to Sharp (1935), was probably introduced westward along the railroads. It ranges from Minnesota to Louisiana, east of the 96° meridian. It may be found in meadows, over-grazed prairies, along railroad rights-of-way, and highways.

Ratibida mexicana is confined to the cool slopes of the Sierra Madre Occidental in the states of Chihuahua and Durango, Mexico (Sharp 1935).

MORPHOLOGY OF THE PARENTAL SPECIES AND HYBRIDS

Ratibida columnaris × *R. peduncularis* var. *picta:* The disc flower of *R. peduncularis* var. *picta* is the largest of the species studied (fig. 1). It has an elongated corolla with a bulbous base, as opposed to the short corolla and non-bulbous base of *R. columnaris* (fig. 7). In the hybrid, the corolla is intermediate in length but has a bulbous base (fig. 4).

The anthers of *R. peduncularis* var. *picta* are much longer than those of *R. columnaris*. Anthers of the hybrid more nearly approach *R. columnaris* in length.

The normally recurved stigma of *R. peduncularis* var. *picta* has numerous inflated hairs extending a considerable distance back from the tip while the stigma of *R. columnaris* has only a few small hairs at the tip. The condition is somewhat intermediate in the hybrid. The style length in the hybrid is intermediate, but because the anthers are more like *R. columnaris*, it extends above them and is exposed.

The corolla lobes are much larger in *R. peduncularis* var. *picta* than in *R. columnaris,* and the hybrid resembles *R. columnaris* in size. The general shape of the palea in the hybrid (fig. 5) is much like *R. columnaris* (fig. 8), with elongation being due, perhaps, to inheritance of the long palea characters of *R. peduncularis* var. *picta* (fig. 2).

The achene of the hybrid (fig. 6) shows a combination of the characters of a fimbriate margin, as in *R. pedunculariis* var. *picta* (fig. 3), and a ciliate margin, as in *R. columnaris* (fig. 9). The hybrid achene has a long corolla stalk on the crown which indicates that disarticulation of the flower in the hybrid is different from that of either parent.

The achene of *R. pedunculariis* var. *picta* has an elaborate wing and protruding pappus. These structures are greatly reduced in *R. columnaris,* and an intermediate condition occurs in the hybrid. The gross morphology of the hybrid achene approaches *R. columnaris* more closely than *R. pedunculariis* var. *picta.*

In *R. pedunculariis* var. *picta* the ligules are either completely purple or purple with a yellow tip. In *R. columnaris* the color varies from completely purple to completely yellow with various intermediates. In the hybrids of these two species the discernible patterns were completely yellow, completely purple, and purple with a yellow tip.

In the greenhouse, *R. pedunculariis* var. *picta* has a limited ability to send up shoots from the roots. It is not known whether this occurs in nature. *Ratibida columnaris* apparently lacks this ability in any situation. It has not yet been ascertained whether this occurs in the hybrid.

Both species usually have nine to 11 leaves on the stem when the first flower opens. The middle leaf of all the plants was selected for comparison. Apical leaves were too immature, and basal leaves were usually incomplete due to partial rotting. The only difference in the two or three leaves on either side of the middle leaf was one of size.

Nine phenotypic classes of leaves representing nine different crosses may be seen in figures 13 through 20. The leaf indicated by figure 11 is from an F_1 hybrid between those plants represented by leaf figures 10 and 12. Leaves indicated by figures 13 through 20 indicate the wide variation one may find in hybrids between these two species. Figures 10 (*R. pedunculariis* var. *picta*) and 12 (*R. columnaris*) are in no way meant to indicate the typical leaves for the species. They are merely parental types.

Table 2 shows a comparison between the two species and their hybrid for characters not represented by the illustrations.

Ratibida tagetes × *R. columnaris:* The corolla of *R. tagetes* (fig. 21) is smaller than that of *R. columnaris* (fig. 27); however, the hybrid corolla (fig. 24) is larger than either parent. Corolla lobes in the parents and the hybrid are about the same. Stamens of the two

TABLE 2.—A Morphological Comparison of *Ratibida columnaris, R. peduncularis* var. *picta,* and the Artificial Hybrid between the Two.

CHARACTERS	*R. columnaris*	Hybrid	*R. peduncularis* var. *picta*
1. Terminal Head			
a) shape	cylindrical	cylindrical to columnar	columnar
b) length (cm.)	1.0–4.5	1.5–5.0	2.0–5.8
c) width (cm.)	1.0–1.7	1.0–1.2	1.1–1.5
2. Ligule			
a) number	4–7	4–7	4–7
b) length (cm.)	1.1–3.6	1.0–2.8	0.7–1.6
c) width (cm.)	0.7	2.5	0.8–2.0
3. Anther length (mm.)	1.25	2.0	2.0
4. Stigma-style length (mm.)	2.25	4.5	5.0
5. Peduncle length (cm.)	5.0–25.0	10.0–36.0	20.0–62.0
6. Pubescence	hirsute to strigose-hirsute throughout, interspersed with resinous glands		
7. Stems			
a) number	1 or more	1 or more	1 or more
b) height (dm.)	2.5–12.0	1.5–14.0	2.5–14.0
c) type	branched	branched to erect and spreading	erect or spreading

parents are approximately the same length, but those of the hybrid are longer than either. Stigmatic hairs, confined to the tips of the stigma in *R. columnaris,* extend down the stigma in *R. tagetes.* In the hybrid they are terminal as in *R. columnaris.*

The palea in *R. tagetes* (fig. 22) has an elongate resin duct in contrast to the oblong-rounded resin duct in *R. columnaris* (fig. 28). This extension or tendency for the resin duct to be somewhat elongate also appears in the hybrid (fig. 25). In the hybrid the pubescence on the palea shows an increase over either of the two parents. Inflated hairs on the margin and apex of the palea are characteristic of *R. tagetes* but not of *R. columnaris.* They are present in the hybrid.

Ratibida columnaris has cilia on the margin and crown of the achene (fig. 29) much like that of *R. tagetes.* However, the callus crown that often shows up in populations of *R. tagetes* (fig. 23) is never found in *R. columnaris.* The hybrid (fig. 26) has an intermediate callus and, in addition, a wing that was not present on either of the parents involved in the cross.

The difference in ligule size may be noted in table 3. The purple and yellow color combination is present in *R. tagetes* as in *R. columnaris*. The writer feels that the genetics involved in the color combinations is the same as in *R. columnaris*. However, the rather small ligules of *R. tagetes* often go unnoticed, probably accounting for the reason that no form or varietal names have been attached to purple color as in *R. columnaris*.

The roots of *R. tagetes* send up numerous stems. This ability is completely absent in *R. columnaris* but is present in the hybrid.

There are 14 to 16 leaves on the main stem of *R. tagetes* when the first head opens, as opposed to nine to 11 on *R. columnaris*. The hybrid had 16 leaves when the first flower opened.

The leaves of *R. tagetes*, *R. columnaris*, and the hybrid are shown in figures 32, 30, and 31, respectively. In *R. tagetes* (fig. 32), the upper two leaflets diverge from the midrib at about a 90 degree angle. These leaflets are smaller than the two below. In *R. columnaris*, the upper two leaflets diverge from the midrib at approximately a 45 degree angle and are larger than the leaflets below. The angle in the hybrid is the same as that in *R. tagetes* but the size of the top two leaflets approaches that of *R. columnaris*.

TABLE 3.—A Morphological Comparison of *Ratibida columnaris*, *R. tagetes*, and the Artificial Hybrid between the Two.

CHARACTERS	*R. columnaris*	Hybrid	*R. tagetes*
1. Terminal Head			
a) shape	cylindrical	rounded-cylindrical	globular to oblong
b) length (cm.)	1.0–4.5	1.4–1.7	0.8–1.0
c) width (cm.)	1.0–1.7	1.0–1.2	0.8–1.0
2. Ligule			
a) number	4–7	5–7	5–7
b) length (cm.)	1.1–3.6	1.5–2.0	0.4–0.6
c) width (cm.)	0.7–2.5	1.0–1.2	0.3–0.5
3. Anther length (mm.)	1.25	1.5	1.25
4. Stigma-style length (mm.)	1.25	1.5	1.25
5. Peduncle length (cm.)	5.0–25.0	2.2–5.5	1.0–6.0
6. Pubescence	hirsute to strigose-hirsute throughout, interspersed with resinous glands		
7. Stems			
a) number	1 *or* more	1 *or* more	numerous
b) height (dm.)	2.5–12.0	3.0	1.5–4.0
c) type	branched	branched at base	branched at base

CYTOLOGY OF THE SPECIES

The chromosome counts of *Ratibida* by Jackson (1959) of meiotic cells and the root tip counts by Perdue (1959) have been verified during this study (fig. 33, 34, and 35).

Meiosis was usually regular in the three species under consideration. However, one plant of *R. peduncularis* var. *picta* had a bridge and fragment at anaphase I in less than 50 percent of the cells. Another plant of this species was found to be male sterile and had 13 instead of 14 bivalents at diakinesis. No seed were set after repeated attempts to cross this plant to other plants of the same species which suggests that it was also female sterile.

Table 4 shows the pollen viability of the parental species and their hybrids. The low viability of the hybrids and the high viability of the parents suggests that the parents were probably not hybrids or hybrid derivatives.

TABLE 4.—Pollen Viability of *Ratibida columnaris, R. peduncularis* var. *picta, R. tagetes,* and Two of Their Artificial Hybrids.*

SPECIES AND HYBRIDS	Code number	Number plants checked	Range	Mean
R. columnaris f. *columnaris*	99	1	98.5	95.1
R. columnaris f. *pulcherrima*	65	1	95.1	95.1
R. peduncularis var. *picta*	27	1	97.1	97.1
R. peduncularis var. *picta*	19	1	98.4	98.4
R. tagetes	29	1	94.6	94.6
R. peduncularis var. *picta*	27			
X		2	60.1–74.2	67.1
R. columnaris f. *columnaris*	99			
R. columnaris f. *columnaris*	64			
X		6	61.0–70.1	67.1
R. peduncularis var. *picta*	153			
R. columnaris f. *pulcherrima*	65			
X		4	68.7–75.7	71.9
R. peduncularis var. *picta*				
R. columnaris f. *pulcherrima*	31			
X		13	58.4–73.2	67.1
R. peduncularis var. *picta*	19			
R. peduncularis var. *picta*	26			
X		2	50.5–57.1	53.8
R. columnaris f. *pulcherrima*	137			
R. peduncularis var. *picta*	27			
X		1	72.3	72.3
R. columnaris f. *columnaris*	118			
R. tagetes	29			
X		1	2.3	2.3
R. columnaris f. *columnaris*	99			

* Percentages based on counts of 300 pollen grains or more.

The root tip chromosomes of three of the four species studied were similar. *Ratibida columnaris, R. pedunculares* var. *picta,* and *R. pinnata* each have three classes of chromosomes. *Ratibida columnaris* ($2n = 28$) has a karyotype similar to *R. pedunculares* var. *picta,* while *R. pinnata* ($2n = 28$) has a karyotype similar to that of *R. columnaris* and *R. pedunculares* var. *picta.* However, a few of the chromosome arms are of a different relative size. Regardless of these minor differences, there are three classes of chromosomes in each of these three species: One large chromosome with a median centromere, nine large chromosomes with a subterminal centromere, and three or four small chromosomes with a more or less median centromere.

Ratibida tagetes ($2n = 32$) has several small chromosomes with a median to subterminal centromere. This genome also contains nine relatively large chromosomes with a subterminal centromere, but it does not have the large chromosome with the median centromere that was found in the three other species.

CYTOLOGY OF THE HYBRIDS

Ratibida columnaris × *R. pedunculares* var. *picta*: Pollen fertility of this hybrid was 50.5 to 75.7 percent (table 4). Heads of 14 plants representing six crosses were studied cytologically for any abnormality during meiosis. Only one cross (65 x 72) showed a very few cells with a bridge and fragment at anaphase I (fig. 37). Other cells from the same plant showed two univalents at interkinesis (fig. 38), thus accounting for the three micronuclei at telophase II (fig. 39) and in the tetrad (fig. 40). Meiosis in the remaining plants was normal (fig. 36).

Ratibida tagetes × *R. columnaris*: Only one plant of this combination was produced. However, the writer feels that other hybrids by the same parental species will act much the same as the one described below.

At diakinesis in many of the cells, 14 bivalents plus two univalents were observed. However, in a few of the cells one of these univalents (fig. 41) was attached to one of the large bivalents. This resulted in 13 bivalents, one trivalent, and one univalent at diakinesis.

At metaphase I, the chromosomes were lined up with one univalent away from the plate (fig. 42), or as many as three away from the plate (fig. 43).

Anaphase I showed a bridge and fragment (fig. 44), a broken bridge and three chromatin structures (fig. 45), a bridge and two chromatin structures (fig. 46), and two bridges and two fragments (fig. 47). It was impossible to determine whether the chromatin structures referred to were fragments or univalents.

Telophase I (fig. 48) often showed a bridge and one or more univalents or fragments not included at the pole.

Figure 49 shows a bridge at metaphase II which had persisted through interkinesis.

In several cells, anaphase II (fig. 50) exhibited two bridges, two fragments, two univalents, and one bivalent.

Telophase II showed four normal-appearing nuclei and four micronuclei (fig. 51), four normal-appearing nuclei and one micronucleus (fig. 52), or three normal-appearing nuclei and five micronuclei (fig. 53). Other abnormal meiotic configurations occurred.

During the formation of the tetrad, some of the micronuclei were included in a cell with a normal sized nucleus. Others formed a wall and became small pollen grains. In several instances up to eight nuclei were formed at the end of telophase II (fig. 53). The percentage of viable pollen was low (table 4) and could be attributed to the various meiotic irregularities that were observed.

DISCUSSION AND CONCLUSION

Sharp (1935), in his study of "The Epappose Genera of the Compositae," has given some profound ideas relating to the ancestry of *Ratibida*. He believed that the ancestral stock of *Balsamorhiza, Iostephane, Zaluzania, Ratibida, Dracopsis,* and *Echinacea* came from two generic complexes.

The *Viguiera* complex is the first discussed by Sharp. The pappose progenators of this group were supposed to have been similar to *Helianthus, Viguiera,* and *Tithonia.* Sharp suggested that *Balsamorhiza, Iostephane, Zaluzania,* and perhaps *Greenmaniella* were derived from this complex. The epappose *Echinacea-Rudbeckia* complex comprised the second generic complex. This group included plants with a more or less columnar or conical receptacle, such as may be found in *Rudbeckia, Echinacea, Dracopsis,* and *Ratibida.* Since the *Echinacea-Rudbeckia* complex is confined mostly to the United States and Mexico, Sharp theorized that it evolved from a similar group of plants that had their origin on the

Appalachian-Ozarkian Upland, an area exposed since the end of the Paleozoic.

Sharp further suggested that *Ratibida* was the more recently derived genus of the *Echinacea-Rudbeckia* complex, and because *Dracopsis* resembled *Ratibida* so much, he believed they had a common ancestry. His reasons for suggesting the more recent origin of *Ratibida* were: (1) the distribution of the genus in a more recent geological territory; (2) the pinnate leaves; (3) specialized seed dispersal; and (4) the aggressiveness and weedy nature of some of the species.

Perdue's mitotic studies (1959) show three classes of chromosomes in *Ratibida columnaris* ($2n = 26, 27$) and *R. pinnata* ($2n = 28$) and two classes of chromosomes in *Rudbeckia* subgenus *Macrocline* ($2n = 36$). Both genera have long chromosomes with more or less median to submedian centromeres. The third class in *R. columnaris* and *R. pinnata* consists of one large chromosome with a median centromere.

Ratibida tagetes ($2n = 32$), a species not studied cytologically by Perdue, has two classes of chromosomes. With the exception of chromosome number, *R. tagetes* has a karyotype similar to *Rudbeckia* subgenus *Macrocline* ($2n = 36$). *Dracopsis* ($2n = 32$) has chromosomes with median and subterminal centromeres. In Perdue's photograph these chromosomes are much shorter than those of *Rudbeckia* subgenus *Macrocline* and *Ratibida*. However, this condition may have been due to different lengths of treatment with colchicine. Since aneuploid change in chromosome number is usually due to a reduction rather than an increase in centromere number (Stebbins, 1950), *Rudbeckia* subgenus *Macrocline* ($2n = 36$) could have given rise to a plant containing $2n = 32$ as in *Dracopsis* and *Ratibida* by a series of translocations.

A reduction in chromosome number may be brought about by a series of unequal, reciprocal translocations, producing short-armed chromosomes which could be lost. The short arms would be expected to contain little or none of the necessary genic material. Judging from comparative morphology and karyotype similarity, a logical progenator for *Ratibida* could be *Rudbeckia* subgenus *Macrocline* ($2n = 36$). However, this discussion is speculative and will remain so until experimental and cytological techniques

uncover more conclusive information as to the origin of the *Ratibida.*

Diakinesis (fig. 41) in the hybrid *R. tagetes* ($n = 16$) $\times$ *R. columnaris* ($n = 14$) showed one of the small chromosomes attached to a large bivalent, suggesting partial homology between one of the large chromosomes and the small one. One might conclude from this that there has been a reduction in chromosome number as a result of a translocation or a series of translocations. Perhaps, these have involved a large and a small chromosome. The small chromosome might eventually consist of a centromere and relatively inert genic material which could then become lost with impunity. The loss of the other chromosome may have come about in a similar manner; however, there is no cytological evidence to support this at present.

Several other aberrations have occurred since the divergence of *R. tagetes* and *R. columnaris.* Non-homology of other chromosomes is indicated by the various figures that appear throughout meiosis. A heteromorphic bivalent at diakinesis (fig. 41) indicated further translocation. A bridge and fragment at anaphase I (fig. 44) are due to a crossover within a paricentric inversion. Two bridges and two fragments at anaphase I (fig. 47) are evidence of further change. Anaphase II (fig. 50) showed two bridges, both of which probably carried over from anaphase I. However, it is possible that one of these bridges was the result of two cross-overs between strands two and three within the inversion and between the inversion and the centromere, with the resulting bridge appearing at anaphase II. Thus one heteromorphic bivalent, one trivalent, and bridges indicate translocations and inversions have taken place.

Meiosis in the hybrid between *R. columnaris* and *R. peduncularis* var. *picta* was not so erratic as the cross just discussed. Fourteen normal-appearing bivalents were observed (fig. 36) at diakinesis in progency of five of six crosses. Progeny of the sixth cross showed a bridge and fragment at anaphase I and two univalents at interkinesis. This type of occasional irregularity may be found within a species. As mentioned earlier, a bridge and fragment appeared at anaphase I in a plant of *R. peduncularis* var. *picta.* The pollen viability of all hybrid progeny involving these six crosses was 50.5 to 75.7 percent.

Abnormality was not observed in meiosis of *R. columnaris* × *R. peduncularis* var. *picta*, but pollen viability was very low compared to that of the parents. One may infer then that "cryptic structural hybridity" (Stebbins 1950) may be involved. Cryptic structural hybridity may be due to a translocation followed by a re-translocation, involving the same segment on two non-homologous chromosomes. If only two of the chromosomes in the genome have undergone change to yield the simplest change possible involving a translocation, the maximum fertility possible would be 50 percent. If more than two chromosomes are involved, fertility decreases.

The inversion-reinversion type of cryptic structural hybridity involving homologous chromosomes in probably the situation in *R. columnaris* and *R. peduncularis* var. *picta*. Here sterility is determined by the percentage of crossing over between the two transposed regions. Fertility may range up to 100 percent, depending on the number of cross-overs. This is assuming that gene deficiency is sufficient to account for sterility. *Ratibida columnaris* and *R. peduncularis* var. *picta* have two similar karyotypes with apparently normal pairing from diplotene throughout the division. However, if it were possible to study pachytene one could probably detect a non-homologous segment on one or more of the pairs.

Since meiosis appeared to be regular in most of the progeny and sterility was 50.5 to 75.7 percent, cryptic structural hybridity involving inversion and re-inversion must have taken place during the origin of the two species.

Inversions, translocations, and differences in chromosome number have been the isolating mechanisms that have arisen during the divergence of *R. columnaris* and *R. tagetes*. Inversions and reinversions have taken place during the evolution of *R. columnaris* and *R. peduncularis* var. *picta*.

Because the chromosomal and morphological differences between *R. columnaris* and *R. tagetes* are greater than between *R. columnaris* and *R. peduncularis* var. *picta*, we may assume *R. columnaris* and *R. peduncularis* var. *picta* are more closely related than *R. columnaris* and *R. tagetes*.

Introgression is probably going on between *R. columnaris* and *R. tagetes* and between *R. columnaris* and *R. pedunculariis* var. *picta*. However, since pollen fertility is so low in the F_1 of *R. columnaris* × *R. tagetes*, introgression is less likely to be as extensive as between *R. columnaris* and *R. pedunculariis* var. *picta*. If introgression is occurring, new genes are being added to the gene pool and increasing the evolutionary possibilities. Because of hybridization within the genus, and because of the great morphological diversity in some of the species, *Ratibida* has great evolutionary potential.

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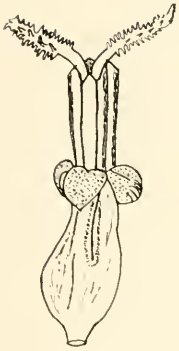
FIGURES 1-9. Flower and fruit structures.
Ratibida peduncularis var. *picta.*
Figure 1. Flower.
Figure 2. Palea.
Figure 3. Achene.
Ratibida columnaris × *R. peduncularis* var. *picta.*
Figure 4. Flower.
Figure 5. Palea.
Figure 6. Achene.
Ratibida columnaris.
Figure 7. Flower.
Figure 8. Palea.
Figure 9. Achene.



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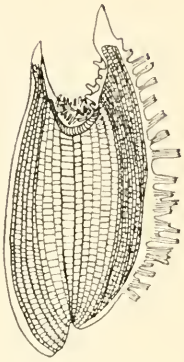

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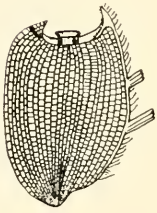

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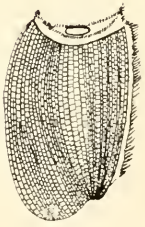

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FIGURES 10-20. Middle leaves of *Ratibida columnaris, Ratibida pedunculares* var. *picta,* and their hybrids.

Figure 10. *Ratibida peduncularis* var. *picta.*

Figure 11. Hybrid between plants indicated by figures 11 and 12.

Figure 12. *Ratibida columnaris.*

Figure 13-20. Hybrid leaves representing eight different crosses.

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FIGURES 21-29. Flower and fruit structures.

Ratibida tagetes.

Figure 21. Flower.
Figure 22. Palea.
Figure 23. Achene.

Ratibida tagetes × *R. columnaris.*

Figure 24. Flower.
Figure 25. Palea.
Figure 26. Achene.

Ratibida columnaris.

Figure 27. Flower.
Figure 28. Palea.
Figure 29. Achene.

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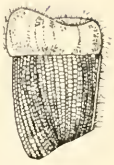

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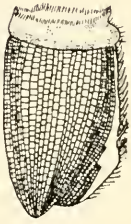

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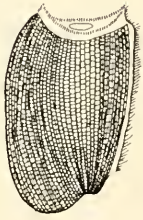

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FIGURES 30-32. Middle leaves of *Ratibida columnaris*, *R. tagetes*, and their hybrid.

Figure 30. *Ratibida columnaris.*

Figure 31. Hybrid between plants indicated by figures 30 and 32.

Figure 32. *Ratibida tagetes.*

FIGURES 33-35. Drawings of meiotic chromosomes.

Figure 33. *Ratibida tagetes* n = 16.

Figure 34. *Ratibida columnaris* n = 14.

Figure 35. *Ratibida peduncularis* n = 14 var. *picta.*

FIGURES 36-40. Drawings of meiosis in *Ratibida columnaris* × *R. peduncularis* var. *picta.*

Figure 36. Diakinesis with 14 normal bivalents.

Figures 37-40. Show meiosis in *R. columnaris* (64) × *R. peduncularis* var. *picta* (153).

Figure 37. Anaphase I, bridge and fragment.

Figure 38. Interkinesis with two univalents.

Figure 39. Telophase II, four large nuclei and three micronuclei.

Figure 40. Tetrad stage with three micronuclei.

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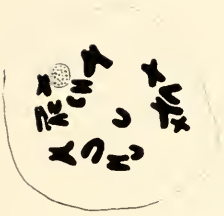

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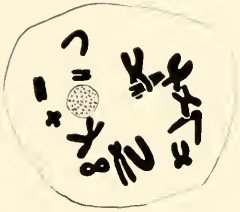

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FIGURES 41-53. Drawings of meiosis in *Ratibida tagetes* × *R. columnaris*.

Figure 41. Diakinesis with 13 bivalents, 1 trivalent, and 1 univalent.
Figure 42. Metaphase I with chromatin structure away from plate.
Figure 43. Metaphase I with 2 chromatin structures away from plate.
Figure 44. Anaphase I with bridge and fragment.
Figure 45. Anaphase I with broken bridge and 3 chromatin structures.
Figure 46. Anaphase I with bridge and 2 chromatin structures.
Figure 47. Anaphase I with 2 bridges and 2 univalents.
Figure 48. Telophase I with bridge and chromatin structure.
Figure 49. Metaphase II with bridge.
Figure 50. Anaphase II with two bridges, 2 fragments, 2 univalents, and one bivalent.
Figure 51. Telophase II with 4 extra micronuclei.
Figure 52. Telophase II with 1 extra micronucleus.
Figure 53. Telophase II with 3 normal appearing nuclei and 5 micronuclei.

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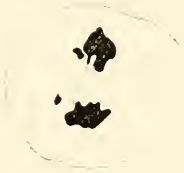

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Immunological and Electrocardiographic Effects of Tissual Components from Chicken Hearts [1]

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ABSTRACT: Antisera produced in rabbits against myosin and cell nuclei from adult chicken hearts inhibited development when injected intravenously into 9- to 11-day-old chicken embryos. Antisera against microsomal, mitochondrial and soluble proteins fractions of chicken hearts were not effective. Quantitative precipitin tests indicated considerable similarity among the antigens in the several kinds of tissual components. Intravenous injection of the tissual components from chickens into rabbits altered their electrocardiograms. Soluble proteins significantly increased the P-R interval, the duration of the QRS complex, and the Q-T interval. Nuclei and microsomes increased the duration of the QRS complex only. Myosin increased the duration of the QRS complex and shortened the Q-T interval. Injections of mitochondria and actin did not influence any of the measurements.

INTRODUCTION

It has been shown that antibodies produced against the tissual proteins of lung, kidney, liver and spleen localize preferentially in the homologous tissue (Korngold and Pressman, '53). Cytotoxic effects of antibodies against tissual proteins have been widely reported. The research reported in this paper was motivated by the assumption that cardiac disease might be induced as a consequence of the cytotoxic action of antibodies on the heart.

Henle, Chambers and Groupe ('41) found that antiheart-muscle serum tested against a sediment of homogenized heart muscle had some homologous reactivity. Kidd and Friedewald ('42), looking for autoantibodies, could demonstrate only weak serologically active

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saline extracts of cardiac muscle from rabbit against normal rabbit serum even though saline extracts of rabbit liver and kidney gave strong reactions with the same serum. Baur ('46) injected antirat heart serum into rats and observed positive reactions. Rapport and Graf ('55) produced antibodies in rabbits against a mitochondrial fraction from rat lymphosarcoma. The antibodies reacted with a mitochondrial fraction from rat intestine, lung, skin, spleen, and stomach but not with the mitochondrial fraction from rat heart. Kaplan ('58) has shown that rabbits injected with saline extracts of heterologous heart develop antibodies that localize in the sarcoplasm. Localized tissue damage can result from injections of homologous antibodies (Landsteiner, '45) and from injections of foreign antisera not related to the tissue under study as shown in the demonstration of lesions in heart, kidneys and arteries of rabbits by the administration of foreign serum proteins (Kobernick and More, '59). Further, injections of foreign proteins not related to vertebrates (meningococcal endotoxin and crude streptomycin proteinase) produce lesions in the heart 48 hours after intravenous administration (Vanace, Wagner, and McGrath, '59).

In our work tissual components of chicken heart have been prepared and antibodies against them have been developed in rabbits. The effects of injections of the tissual components on the electrocardiograms of rabbits' hearts were studied. The antisera against the tissual components were used in *in vitro* precipitin studies to measure the serological correspondence among the tissual components from adult chicken heart and in *in vivo* tests to kill embryonic chicks.

MATERIALS AND METHODS

Preparation of Antigens

Cleaning of Heart Tissues. As soon as chickens were killed, their hearts were placed in cold (5 to 10°C.) chicken Ringer's solution (Romanoff and Romanoff, '49) and were kept under refrigeration over night. Fat deposits were trimmed away; the auricles were removed; the pericardial membrane was pulled off; the coronary arteries were teased out; the ventricular cavities were opened and columnae were cut out. The myocardium of the ventricles was rinsed in water and was used immediately or was placed in chicken Ringer's solution and was stored at — 20°C.

Fractionation. Four fractions of chicken heart were prepared by a technique (Fig. 1) of differential, high-speed centrifugation derived from the methods of Claude ('46), Cleland and Slater ('53),

Allfrey ('54) and DeDuve ('54). This fractionation technique yielded four fractions: nuclear particles, labeled S-2; sarcoplasmic particles, labeled R-1 (mitochondria) and R-2 (microsomes or membranes of the ergastoplasm); and sucrose soluble proteins, labeled S-1. The entire fractionation was carried out at 0 to 5°C.

Each fraction was observed microscopically at 900 × for purity. Methylene blue at 0.1% concentration was used to aid in identifying nuclei and cytoplasmic constituents.

Syringing. After centrifugation at the high speeds used in the fractionation the pellets of residues are frequently firm and difficult to suspend by stirring. A homogenous suspension of particulate material is necessary for adequate washing and for uniform sampling. Homogenizing the pellets in a teflon grinder might have the undesirable effect of further rupturing the particles of a fraction. A technique of syringing, modified from Klein and Johnson ('54) and Brillaud ('58), was employed to maintain the integrity of particles isolated in a fraction and to provide satisfactory washing and suspension.

Syringes of 10 or 50 ml. capacity, depending upon the volume to be suspended, were used. A pellet was first broken up in a partial volume by syringing for one minute using a three-inch, 15-gauge hypodermic needle. Then a three-inch, 23-gauge needle was used, syringing for five minutes at the desired final volume. The bevel of the needle was always kept below the surface of the fluid and the syringing pressure was kept low to prevent denaturation associated with foaming of the proteins.

Preparation of Myosin and Actin. Myosin and actin from the muscle of chicken heart were prepared (Fig. 2) using a technique devised by Szent-Gyorgyi ('51) and modified by Tsao and Bailey ('53). This technique allows the extraction of the two proteins from the same tissue sample. The entire preparation of the myosin and actin proteins was done at 0-5°C.

Solubilization of Antigens. Some of the serological tests employed in our work required soluble proteins. The nuclear, mitochondrial, and microsomal fractions as prepared by differential centrifugation are particulate in nature. Consequently, two techniques for the solubilization of particulate protein systems were utilized. One method was a modification of the Cohen, Levi-Montalcini and Hamberger ('54) technique using streptomycin sulfate (Fig. 3). The second method utilized a Raytheon sonic oscillator at 80 volts output, 130 volts plate. After 30 minutes in the vibration chamber the

fractions were centrifuged at 30,000g for 30 minutes. It is possible that the solubilized solution obtained by sonic oscillation could contain protein systems in a true solution or in a fine colloidal suspension. The final solutions were analyzed for protein nitrogen by the micro-Kjeldahl technique and used as antigen solutions for *in vitro* tests.

Antisera. All antisera were produced in healthy adult rabbits. Antisera were prepared against myosin, actin, nuclear fraction, mitochondrial fraction, microsomal fraction, and soluble proteins fraction from heart muscle of chickens. Injections were subcutaneous into the nape of the neck and intraperitoneal into the lower median region of the abdomen.

Typical examples of the injection schedules are given in Table I. The total number of antisera prepared and used in this study was 18. There were two antisera prepared against myosin; three against actin; four against nuclear particles; three against mitochondrial particles; three against microsomal particles; and three against soluble proteins from fractionation. Other antisera used for control purposes were taken from laboratory stock.

The usual procedure for an injection schedule was to give one injection of 0.5 ml. subcutaneously and then to give one injection of a larger quantity (3.0 to 5.0 ml.) one week later intraperitoneally. It was customary to give the first injection as an emulsion. The emulsion was prepared as one part of the preparation of protein and one part Freund's adjuvant or one part emulsion oil. For the other injections the proteins were given as prepared.

Seven days after the second injection the rabbits were bled of 50 ml. by cardiac puncture. On the day of the bleeding the large dose of antigen was injected to start another series. One week later the large dose was repeated. After seven days the rabbits were again partially bled and the large injections repeated. The blood drawn at each bleeding was processed for its serum. This schedule was continued until 100 ml. of antiserum had been collected. The serum, diluted in an equal quantity of buffered 0.85% saline, was sterilized by Seitz filtration and stored at — 20°C.

In Vitro Serological Tests

In order to verify the activity of the antisera and to characterize the specificity of the antisera, three *in vitro* tests were run: the Ouchterlony agar-plate precipitin test (Leone, Leonard and Pryor, '55); a turbidity measurement of an antigen dilution series (Leone, '49); and a Nessler quantitative measurement of an antigen dilution series (Lanni, Dillon and Beard, '50).

Most of the activity of antibodies produced against tissual proteins has been measured by the complement fixation technique (Kidd and Friedewald, '42 and Kaplan, '58). However, Brillaud ('58) found complement fixation tests of little value in serological studies on tissual antigens because of the high anticomplementary action of the extracts from the tissues. Also, since the precipitin tests are simpler not only in mechanics but in evaluation of results, the complement fixation technique was not employed.

Precipitin Tests. Antiserum was placed in the center well of the Ouchterlony agar plates and the six antigen solutions, myosin, actin, nuclei, mitochondria, microsomes, and soluble proteins, were placed in the six peripheral wells. Each day the plates were checked for zones of precipitates. When precipitates became visible, photographic records were made of the plates daily. After seven days the plates were discarded.

Two doubling dilution series of each antigen were prepared as described by Leone ('49). One series was prepared for turbidity measurements and the other series was prepared for quantitative Nessler determinations of the antigen-antibody precipitates. Aliquants of stock dilutions were set up so each antigen could be tested with its homologous antiserum and with heterologous antisera. All 18 antisera prepared for this study were tested. Each tube of the tests contained 1.8 ml. antigen solution and 0.2 ml. antisera.

In Vivo Serological Tests

Relative Hatchability. Embryonated chicken eggs were injected with various antisera to determine the influence of these antisera on hatchability of embryonic development. The eggs were injected after nine to 10 days of incubation at 37° C. and returned to incubate until they had time to hatch between the 20th and 24th day of incubation. After being injected, the eggs were checked daily. Eggs which were not viable when checked and those which had not hatched by the 25th day of incubation were opened and examined for bacterial contamination. Tubes of thioglycolate bacterial culture medium were inoculated with material taken by sterile stabs into the eggs. Embryos from eggs which were not infected were judged to have been influenced by the material injected if they died within four days after injection. Embryos which hatched and embryos which developed four days or more after injection were judged to be uninfluenced by the material injected.

To measure the influence of each antiserum upon the viability of the embryos a hatchability-ratio of all embryos which hatched, or developed beyond four days after injection, to all uninfected eggs injected was established. In order to account for mechanical effects such as hemorrhage (Vieuchange, Robbins and Enders, '50) the hatchability-ratio for the control group that received chicken Ringer's solution was assigned the relative hatchability of 1.0.

Injection Technique. Eggs which had been incubated for nine to 10 days were candled for viability by observing the movement of the embryo. The locations of any large blood vessels near the air sac were marked on the shell with a wax pencil. The surface of the egg was scrubbed with 70 percent ethanol. For intravenous injection, a triangular wedge, approximately one-half inch on each side, was exscinded from the egg shell over one of the marked blood vessels by means of a high-speed dentist's drill and a circular burr (Walter, Allmann and Mahler, '56). The wedge was pulled away from the shell membrane by jeweler's forceps. The membrane must remain completely unruptured to prevent bacterial contamination of the egg. A drop of sterile mineral oil was placed on the intact membrane so that it was made transparent. If the egg was not viable or the membrane had been perforated, the membrane remained opaque. The injection was always toward the air space, away from the embryo.

The injections were performed using one-half-inch, 30-gauge needles. The shaft of the needle was bent to facilitate the handling of the syringe and insertion of the needle into the blood vessel. Antiserum was introduced into the lumen of the vessel, through the shell membrane, with the bevel of the needle up. Each embryo received 0.2 ml. of antiserum. The triangular wedge of the shell was replaced and sealed using hot paraffin.

The eggs which received antiserum into the yolk-sac were injected at the narrow end through a small hole prepared by a high-speed drill. Needles of 23-gauge were used to place the inoculum near the embryo. Each egg received 0.5 ml. of inoculum. The hole was sealed with paraffin.

Aseptic conditions were maintained in both techniques involving the use of embryonated eggs.

Electrocardiography

An effort was made to measure the influence of tissual components from chicken hearts upon the electrical field of the hearts of rabbits. The assumption was that the antibodies which a rabbit produced in

response to the injections of homologous tissual components from chicken would be sufficiently aspecific to localize in the rabbit's cardiac tissue. The antibodies would interact with cardiac components of the rabbit so as to cause injury and would alter the tracing of the electrical wave sufficiently to be measured by electrocardiography.

A direct-writing Burdick EK III Dual-speed Electrocardiograph was used to record electrocardiograms (ECG) of rabbits. The combination of leads from animal limbs was keyed to the recommendations of the American Heart Association for clinical ECGs (Katz, '46).

If a precordial lead was required in a combination it was placed as centrally as possible on either the left or right rib cage. Leads I, II, III, aVR, aVL, and aVF were used routinely. Occasionally, precordial leads CR, CL, CF and V were taken from left side and right side.

The animals were placed on their backs and secured. The right and left fore limbs and the right and left hind limbs were shaved. To facilitate wetting of the skin the cleared regions were bathed with 70 percent ethanol. A slurry of supersaturated NaCl or commercial electrode jelly was rubbed onto the areas for proper conduction of the electrical potential to the electrode. Silver wire was used for electrodes. The wire was wrapped around a limb three or four times. The wire coil was positioned over the prepared region and tightened. Leads from the electrocardiograph were attached to the appropriate electrodes by alligator clamps. The electrocardiograph was adjusted to give one and one-half centimeter deflection in response to the standard one millivolt. ECGs were recorded at 25 and 50 millimeters per second. The ECGs were coded and were analyzed as follows:

Tracings of Leads II or III were selected from each ECG for analysis because the detail of electrical waves was best in these leads. Figure 4 shows an illustrative tracing of the electrical activity of a heart through two cycles. The component waves of one cycle are marked above the tracing and three measurements selected in ECG analysis below. The three measurements are the P-R interval, duration of the QRS complex, and the Q-T interval. All three measurements are expressed in milliseconds. The P-R interval was measured from the beginning of the P wave to the onset of the QRS complex. Duration of the QRS complex was measured from the beginning to the end of this complex wave. Q-T interval was measured from the onset of the QRS complex to the end of the T wave.

RESULTS

Antigen Preparations

Fractionations. Microscopic observation of the fractions of chicken heart after high-speed differential centrifugation (Table II) was used to determine the degree of separation of the fractions. Whole cells, tissue fragments, fibers and other forms of cellular debris were isolated into a waste fraction (R-VII). In this fraction (R-VII) and in the nuclear fraction, nuclei appeared as short rods of deep stain with methylene blue. Contamination of the nuclear fraction by mitochondria and microsomes did not occur in both stained and unstained preparations as evidenced by the lack of oval globules in the fraction. There was some mutual contamination of the mitochondrial and microsomal fractions by small, lightly-stained oval globules. However, the globules were not visible in the unstained microsomal fraction although brownian movement was evident in the undifferentiated background. Only the soluble proteins fraction demonstrated lack of visual particles. Even the undifferentiated background was without brownian movement or stain in the soluble proteins fraction.

Myosin and Actin. Proteins extracted from chicken hearts were not checked visually for purity. The only observation taken on the condition of actin and myosin was that actin remained in solution after thawing and that once thawed, the myosin solution contained a great abundance of precipitate. The precipitate was denoted by its integrity. In order to break up the precipitate, which appeared as a gelatinous mass of tissue, three minutes of mincing in a Waring blendor was required. Even the mince was not uniform. The supernatant indicated a protein concentration greater than 1% in presumptive protein tests using sulfosalicylic acid. At room temperatures, myosin solution also formed a precipitate, but the precipitate was easily suspended by slight agitation. The precipitate was assumed to be myosan (Hawk, Oser and Summerson, p. 232, '47).

Antisera Production

No apparent change was found in the rabbits' general health after injection of the homologous tissual fractions or proteins from chicken heart. Four of the 18 rabbits died during the stress of cardiac bleeding. Autopsy revealed large auricular tatters in these four hearts. A fifth rabbit was sacrificed early because it developed a large skin tumor. Site of the tumor was unrelated to the sites of injection.

In Vitro Serological Tests

Solubilization. In the materials solubilized by streptomycin sulfate, presumptive protein tests using sulfosalicylic acid showed no protein in the mitochondrial and microsomal fractions and less than 0.1% protein in the nuclear fraction. Consequently, these fractions were not used. Solubilization by sonic oscillations yielded solutions of satisfactory protein concentration, 0.1% or more. A solution of actin was not available for testing with most of the antisera. Some actin was used in the Ouchterlony agar-plate testing.

Turbidimetric and Quantitative Precipitin Tests. The results of *in vitro* testing of the antisera are recorded in Tables III and IV. Data obtained from the reactions of antisera with diluted sequences of antigens were plotted as serological activity versus antigen concentration. The data for turbidimetric serological tests were plotted separately from quantitative Nessler measurements. Some of the serological curves demonstrated maximum precipitates or peaks in the range of antigen concentration employed. Antisera against myosin had two peaks with the soluble proteins fraction. In a number of reactions the precipitates steadily ascended toward a peak at higher antigen concentrations than those compared. Particulate microsomes did not reach a peak with any antiserum.

To designate the relative reactivity of an antiserum with the antigens, the area under each serological curve for that antiserum is represented by a ratio (Table III). The homologous reaction is assigned the value of 1.0 and all heterologous reactions are adjusted accordingly. The curves are compared only through equivalent ranges of antigen concentrations. The homologous reaction is not always the strongest. Particulate mitochondria show the weakest reactivity with all the antisera tested by means of the quantitative Nessler's technique. Microsomes, solubilized by sonic oscillation, react as the weakest antigen with all antisera tested by turbidity. Generally, the strongest reactions are obtained with the nuclear fraction, both in its particulate state and in its solubilized form. Only the reaction of the antisera against microsomes with myosin is higher than the reaction with particulate nuclei. Nesslerization measurements show that the five antigens react in a different order with each antisera indicating some specificity of the antisera. From the turbidimetric data of Table III it is seen that the five antigens react in the same order with antimitochondria, antimicrosomes and antimyosin.

Agar-plate Tests. The results of Ouchterlony agar-plate tests are given in Table IV. None of the antisera developed precipitates with solubilized mitochondria or with microsomes. Many antisera reacted with the soluble proteins fraction in such a way as to display two or three zones of reactivity, of which, one zone was long and very thick and the other one or two short and thin. The antinuclei reaction zone with myosin demonstrated complete identity to the zone with solubilized nuclei and to the thick zone with soluble proteins. The reaction of myosin with antimicrosomes showed complete identity to the reaction zone of solubilized nuclei and partial identity to the thick reaction zone of soluble proteins. With antimyosin, the reaction zone of myosin showed complete identity to the reaction zone of solubilized nuclei. The reaction zone of actin with antiactin VB2259 demonstrated complete identity to the reaction zone of myosin. With antiactin VB2559 the reaction zone for actin has complete identity to the thick reaction zone of soluble proteins. Myosin shows complete identity to solubilized nuclei and partial identity to the thick reaction zone of soluble proteins with the antiactin serum. With this antiserum soluble proteins and chicken plasma show complete identity to all zones of reaction.

In Vivo Egg Tests

Two or three dozen eggs were injected in the yolk sac with each antisera and with control sera and chicken Ringer's solution. Control sera did not adversely influence the survival of the embryos since 90 to 100% of the eggs in all groups hatched.

Table V shows the results obtained from the intravenous injections of various antitissual antisera into embryonated eggs. Eggs which hatched or developed for four days beyond the time of injection were considered not to be influenced by the material injected. In order to adjust for the traumatic influences of intravenous injection—rupture of the blood vessels, hemorrhage of the capillaries in the vitelline membrane, or tearing of the shell membrane—the proportion of hatchings obtained from injection of chicken Ringer's solution was assigned a value of 1.0. The proportion obtained as a result of injecting antisera and control sera were related to this value. Antimyosin VB5558 had relative hatchability or a survival value greater than unity which indicated that this antiserum did not adversely influence survival. This same antiserum plus antimitochondrial antiserum reduced the survival value to 0.5. Note that control sera reduced the survival value to 0.7. Only those antisera which reduced the survival value to one-half of the value for control

sera were considered to have affected the embryos in a specific manner. Antinuclei serum VB2359 and antimyosin serum VB359 were the only antisera to demonstrate activity in excess of that of normal rabbit sera.

Electrocardiography

Some of the early electrocardiograms had interference from loose contact by the electrodes to the skin. Satisfactory contact of electrodes on the chest was never established. Consequently, injuries occurring perpendicular to the frontal plane through the heart were not measured.

Measurements from ECGs were taken and analyzed statistically (Table VI). It was assumed that injury induced by injections of homologous tissual components would not influence heart rate since injury of cardiac tissue would not influence the pace-maker, the sino-auricular node. The rapid or slow heart rates would be responses to vagus stimulation resulting from the handling of the rabbits. Mean heart rate for all rabbits was 260 beats per minute. Three standard deviations from the mean was $\pm$ 45 bpm. Probability for a heart rate greater than three standard deviations being part of the sample was 0.001. The ECGs of rabbits whose heart rates were greater than three standard deviations from the mean were not analyzed statistically. Measurements from the ECGs of these rabbits were considered individually.

Because of the small number of experimental and control rabbits (that is, 1 to 6) and because the experimental and control groups had different numbers of individuals the "student's" *t*-distribution test (Snedecor, '57) was employed to calculate the probability (P) value for the mean of the measurements taken from the ECGs. Only those measurements for the experimental groups having a probability of 0.050 or less were considered significantly different from the mean value of the control group.

The physiological importance of each measurement was taken from Katz ('46) and Dimond ('58). Prolongation of the P-R interval indicates either acute rheumatic carditis, arteriosclerotic heart disease or digitalis therapy in medicine. A shortened interval is thought to be the result of an aberrant conducting mechanism—the bundle of Kent—associated with the bundle of His. Only the values of one statistically-tested rabbit, which, incidentally, was injected with the soluble proteins fraction, were significantly different from the value of the control rabbits for the P-R interval. All the other

experimental groups of rabbits had probability values greater than 0.050 so that they were within the range of values of the control group.

The QRS complex represents the duration of the depolarization of the bundle of His, the Purkinje network and the ventricular musculature. Increased duration of QRS can be due to ventricular hypertrophy or due to the branches of the bundle of His being blocked, and may require the conduction of the electrical impulse by some other route, usually by the musculature. All groups showed an increase in QRS duration and most of these were significantly increased. The probability was less than 0.001 that the increased QRS duration in rabbits which received nuclei, microsomes, soluble proteins and myosin could be within control variation. Only rabbits inoculated with mitochondria and actin were within the 0.050 P limit.

The Q-T interval measures the total time required for depolarization and repolarization of the ventricles. Decreased Q-T interval is commonly found in hyperparathyroidism and digitalis therapy. Increased Q-T interval is frequently seen in electrolyte disturbances resulting from renal malfunction, in myocardial ischemia and infarction, in various toxic states such as rheumatic carditis and diphtheria, and in ventricular hypertrophy. One rabbit receiving soluble proteins had a significantly prolonged Q-T interval, while the two rabbits in the myosin group had a shortened interval.

There was one rabbit from each group injected with mitochondria, microsomes, and soluble proteins which was excluded from statistical testing because the probability was less than 0.001 that its heart rate was within the control value. Two of these rabbits had a slower heart rate than the control rate (260 beats per minute) and the third rabbit a faster rate. Normally slower heart rates concomitantly increase the P-R interval and the Q-T interval. Heart rate does not influence the duration of the QRS complex significantly.

One rabbit (VB559) which received injections of mitochondria had a heart rate of 180 bpm. This rabbit had a P-R interval of 50 msec which probably should be considered short since the value was even less than that for the control group. The Q-T interval was longer (160 msec) than the value for the control group and probably represents a normal expression. The probability that the QRS duration (30 msec) of this ECG is part of the control group was less than 0.001.

Rabbit VB659 which was injected with microsomes had a fast heart rate (360 bpm). The P-R interval for this rabbit's heart was short (50 msec). A short Q-T interval, 110 msec, was obtained. Both short intervals are expected because the heart rate was fast. Duration of the QRS complex did not differ from the control value.

The third rabbit excluded from the statistical testing received soluble proteins injections and had a slow heart rate of 190 bpm. This rabbit's P-R interval was equal to the control value (70 msec), but a longer interval was expected because of the slow heart rate. The Q-T interval was longer (180 msec) than that value for the control group, an expected result. The QRS complex duration was significantly greater (30 msec) than that value for the control group.

A P wave was never found in Lead I for any rabbit. The QRS vector was associated primarily with Lead II and the T wave vector with Lead aVF. The P wave and T wave were always inverted in Leads aVR and aVF. A Q wave always occurred in Leads aVR and aVL and sometimes in other Leads. These observations indicate that the electrical axis of a rabbit's heart is anteroposterior.

DISCUSSION

In Vitro Serological Tests

The differential centrifugal fractionation scheme used in this work produced antigenic fractions of cellular components from chicken hearts. Myosin and actin extracted from heart muscle of chickens as described in this work were also antigenic.

Of the two techniques used to quantitate the precipitin reactions, quantitative Nessler's and turbidity, the more valuable measure of serological correspondence among the antigens was obtained by the Nesslerization technique because this method utilized the same particulate preparations which were used to stimulate antibody production, whereas, the turbidity method employed only the solubilized fractions as antigens. Quantitative measurements of the precipitin reactions showed some serological correspondence among the nuclear, microsomal and soluble protein fractions and myosin (Table III). However, it was difficult to interpret the results because all the serological curves did not attain peaks through the range of antigen concentrations which was used for comparisons. In spite of the difficulty of interpreting the curves, the mitochondrial fraction did not show correspondence to any of the other antigens. Mitochondria, moreover, were poorly antigenic and reacted only slightly with antisera produced against them.

When solubilized fractions were compared by means of turbidimetric serological tests, the order of reactivity with each antisera changed from that obtained using particulate antigens and the Nesslerization test. Notably, the solubilized mitochondria were the second strongest reacting fraction with each antisera instead of being the weakest. One explanation of the change in the order of reactivity could be that solubilization of the particulate fractions would make new combining sites available for reaction. Nuclei and mitochondria would be expected to release or expose complex protein systems not available for serological activity prior to solubilization because of limiting membranes surrounding them. Peters ('57) demonstrated serologically a serum albumin precursor in mitochondrial and microsomal fractions when they were solubilized by means of desoxycholate. Solubilization, then, could account for the change in the position of reactivity for the mitochondrial fraction with the antisera as measured by the two techniques. However, microsomes represent a mosaic or a wide variety of small configurations of the ergastoplasm created during homogenization. It is doubtful that sonic oscillations could increase the number of kinds of reactive substances. Another explanation of the change in the order of reactivity could be that the two serological techniques provide different kinds of measurements of the same intermolecular reactions; for example, the quantitative Nessler's technique might be more sensitive to molecular combinations large enough to be sedimentable in a low centrifugal field while the turbidity technique might be more sensitive to the same kind of molecular combinations but of smaller size. Assuming the reality of the mosaic nature of the ergastoplasm after homogenization, it is probable that the measurements taken by the two techniques indicate different quantitative expressions of the same intermolecular reactions rather than indicate a qualitative difference due to solubilization. Also, if the two techniques measured the same serological reactions, then the relative position of the reactions of soluble proteins and myosin with each antisera should be similar because the same preparations of these two antigens were used for both techniques.

That no reactions could be demonstrated by the Ouchterlony agar-plate technique (Table IV) for the mitochondrial and microsomal fractions against any antisera might be due to the concentrations of the fractions being so low that a visable reaction could not be shown by the technique. However, serological correspondence among actin, myosin, and nuclei was demonstrated clearly. Some

correspondence between these protein systems and soluble proteins also was indicated.

It is clear that the serological reactions of the antisera developed in this work are specific for tissual components because none of the antigens reacted with normal rabbit sera. The reaction of antibodies induced by the soluble proteins fraction with chicken plasma would be expected because the chicken hearts were not perfused and the soluble blood proteins could be present as a contaminant in the soluble proteins fractions used in antisera production. The extraction procedure for actin (Fig. 2) precludes contamination by blood proteins. An explanation for the observed reaction between anti-actin and chicken plasma could be that actin or actin precursor are normally present in serum.

In Vivo Serological Tests

An explanation for the failure of antisera injected into the yolk sac to bring about reduction in hatchability is that the small quantities of antisera were greatly diluted with yolk so that effective amounts of antibodies did not reach the embryos. Injection of antisera intravenously into embryos were effective probably because the antibodies were only slightly diluted with a small blood volume. Also, the antibodies could be carried directly to the homologous organ or some other critical site in the embryo. *In vivo* tests (Table V) of antisera against tissual components from chicken hearts show that only antisera against nuclei and myosin had adverse effects of any magnitude as measured by relative hatchability.

Relative hatchability of chicken eggs injected with antisera is a critical test of the biological effect of homologous antibodies. The computation of relative hatchability allows for the mechanical effects of intravenous injection (Vieuchange, Robbins and Enders, '50). Further, while the effects of vascular lesions produced by the injections of foreign serum (Campbell and Santos-Buch, '59, and Kobernick and More, '59) have not been taken into calculation, these effects were considered by comparing the relative hatchability value for injections of control rabbit antisera against values of homologous antisera.

The organ specificity of the antisera cannot be determined from the relative hatchability data. It is possible, for example, that death of the embryos resulted not from cytotoxic reactions with heart but from nephrotoxic reactions similar to those known to result from injections of other antiorgan sera, such as antilung and antiplacenta (Korngold and Pressman, '53, and Mellors, Siegel and Pressman,

'55). Data on organ specificity of the antisera can be obtained only by localization studies using isotope or fluorescein labeled antisera (Pressman, Yagi and Hiramoto, '58). Although other organs may have been influenced by injections of antigens used in our study, the ECGs indicated that the antibodies induced by injections of tissual antigens from chickens had some affinity (specificity) for cardiac tissue of the rabbit. Consequently, the rabbit antisera, injected into chicken embryos probably acted directly on the embryos' hearts to bring about death.

Injections of homologous tissual components into rabbits altered the electrical activity of their hearts as measured by the electrocardiograph (Table VI). The soluble proteins fraction increased the duration of the P-R interval, the QRS complex and the Q-T interval. Myosin increased the duration of the QRS complex and the Q-T interval. Nuclear and microsomal fractions increased the duration of the QRS complex. The mitochondrial fraction and actin did not influence the duration of these intervals. The ECG alterations that were observed are explained as follows:

Campbell and Santos-Buch ('59) injected large quantities of horse serum into rabbits. They found many lesions in the heart and only a few lesions in the lung, kidney, and aorta. Myocarditis was associated with or without necrosis and scarring, but with little hypertrophy of the muscle. Kobernick and More ('59) injected horse serum with ACTH and cortisone into rabbits subjected to the stress of cold. They concluded that the granulomatous lesions of the heart valves were not due to the "general adaptation syndrome" in response to a nonspecific "stress" but by the state of hypersensitivity induced by sensitization of rabbits with massive doses of foreign proteins. Their antigen (horse serum) was from the blood system; consequently, the resulting antibodies should localize throughout the circulatory system, including the heart. Injections of the heart muscle proteins from chicken hearts prepared for our work bring about changes of the ECG because the rabbits produce antibodies against these proteins. A possible state of hypersensitivity of the rabbits would bring about a quantitative production of antibodies greater than necessary to react with the injected quantity of antigen. The excess quantity of antibodies would react *in vivo* with heart proteins of the rabbits similar to heart proteins of the chickens and cause lesions. Hypertrophy of the cardiac tissue could result from fibroplasia of the lesions. Fibrous tissue is a poor conductor of electrical impulses (Dimond, '58). It would seem reasonable, then, that changes in the duration of the ECG intervals used in our work are due to loss in the conduction efficiency of the musculature.

Hypothesis

The mitochondrial fraction was the only antigen which did not seem to bring about any physiological damage as measured by embryo hatchability or electrocardiography. Even though the ECGs of two of the rabbits injected with mitochondria did not indicate any change, these rabbits did produce antisera having measurable reactivity *in vitro*. One explanation for this contradiction is that the circulating antibodies were not taken in through the cell membrane where the antibodies' specifically reacting organoid was located. However, some studies reported by Kaplan ('59) indicate that circulating pathologic antibodies localize within the myofibers of human hearts. Also, if hypertrophy of heart muscle is due to fibroplasia of lesions caused by nonspecific antisera, then injections of mitochondria should have influenced the ECGs.

A more reasonable explanation and the thesis of this presentation is that the antibodies against the different protein systems used in this work have different reacting sites and these sites determine the mode by which physiological damage can be expressed. The reasoning for this follows.

Gay ('60) has speculated from electron microscopic work that a special region of a chromosome confers specificity by depositing desoxyribo- and ribonucleic acid upon a section of the nuclear membrane. This section of the membrane is released into the cytoplasm and becomes a part of the ergastoplasm, carrying a particular nucleic acid (of RNA derivation) designed to direct the synthesis of a particular protein within the cytoplasm.

Peters ('57) showed that the mitochondrial and microsomal fractions of the rat liver possess a precursor to serum albumin bound with nucleoprotein. Both cellular fractions were solubilized with desoxycholate. When considering homogenized tissual preparations that have not been solubilized, it is likely that this nucleoprotein intermediate for serum albumin would be contained within the limiting membrane of mitochondria and hence, would not be detected by circulating antibodies. Microsomes, because of the manner in which these particles form (Palade, '58), would maintain the precursor on their exterior surface and, consequently, be available for serological reaction *in vitro*. The soluble proteins fraction from homogenizations would contain the serum albumin-nucleoprotein precursor which was removed from the microsomes by the mechanical effects of homogenization as well as serum albumin spontaneously released from the precursor complex.

Hence, if fractions of liver were used to induce antibodies, the nuclear, microsomal and soluble proteins fractions would contribute the same antigen, the nucleoprotein intermediate for serum albumin. While mitochondria contain the same antigen, it is not presented to the antibody-producing mechanism.

If cardiac tissue had a secretory function then a site could be postulated for the serological reaction *in vivo* of antisera against nuclei, microsomes, and soluble proteins from heart. Ebert ('58) reviewed the work of Peters ('57) and Sterzl and Hrubesove ('57) and suggested that a nucleoprotein intermediate for myosin might be present in cardiac tissue. In the work reported in this paper, *in vitro* and *in vivo* serological interactivity of cardiac myosin and nuclear, microsomal and soluble proteins fractions has been indicated. Assuming a nucleoprotein intermediate for myosin then the physiological action, intracellularly, of circulating antibodies against these different antigens probably occurs in two sites, the sarcoplasm and the myofilaments of heart muscle.

One site, in the sarcoplasm, is sensitive to the antibodies directed against the myosin-nucleoprotein precursor. The mode of expression for this reaction would be the impairment of the electrical conductivity of the myofiber as measured by electrocardiography.

The second site, in the myofilament, is sensitive to antibodies against myosin. This reaction would be expressed as the failure of chicken embryos to hatch because the myofilament is tied to antimyosin so that the myofiber cannot contract. Prolonged exposure of rabbits to injections of myosin would cause cardiac trauma to the extent that death would result. The antibodies against the myosin-nucleoprotein intermediate would not react with mitochondria *in vitro* or *in vivo* because of the limiting structure of mitochondria which protects the internal proteins systems from circulating antibodies.

Similar mechanisms to those described above for physiological damage from actin or antiactin injections might be operative. The Ouchterlony tests (Table V) show correspondence among all antigens against antiactin except mitochondria and microsomes which did not react with any antisera measured by this technique. However, no physiological damage, as detected by relative hatchability and ECG measurements, was related to actin or its antisera.

In vivo, mitochondria would be affected by mitochondrial-specific antibodies, but not by the antibodies against myosin and myosin-nucleoprotein intermediate. Because mitochondria are not as intimately associated with the sarcolemma as the ergastoplasm or the

soluble proteins of the sarcoplasm, any effect from reactions with antibodies probably would not influence the electrical conduction of the myofiber. Also, any reaction with mitochondrial specific antibodies possibly would not bring about cell death because the antibodies would be specific for and localized on the outer limiting structure of the mitochondria, consequently, not inhibiting the internal metabolic processes.

SUMMARY

1. Tissual components from adult chicken heart were prepared. These included the contractile proteins of muscle, myosin and actin, and the cellular fractions, nuclei, microsomes, mitochondria and soluble proteins.

2. Antisera were prepared in rabbits against the component proteins separated from adult chicken hearts.

3. *In vitro* serological comparisons were made of the cardiac protein-components using three techniques for measuring the precipitin reaction. One technique, Nessler's quantitative measurement, indicated serological correspondence among myosin and the nuclear, microsomal, and soluble proteins fraction. The mitochondrial fraction was weakly antigenic. When mitochondria were solubilized and a second technique (turbidimetric) was used, their reactivity with all antisera in relation to the other antigens increased greatly. Ouchterlony agar-plate tests indicated qualitative serological equalities among actin, myosin, nuclei, and soluble proteins. No reactions were observed for these antigens with control rabbit sera. Mitochondria and microsomes did not react with any antisera in the agar-plate tests.

4. Antisera to the chicken heart proteins were injected intravenously into nine- to 11-day-old chicken embryos. Of the antisera injected, antinuclei and antimyosin inhibited embryonic development enough to be considered effective.

5. Electrocardiograms were taken on the rabbits which received injections of the chicken heart proteins. Of the antigens injected, mitochondria and actin did not influence any of the measurements. Soluble proteins significantly increased the P-R interval, the duration of the QRS complex and the Q-T interval. Nuclei and microsomes increased the duration of the QRS complex only. Myosin increased the duration of the QRS complex and shortened the Q-T interval.

6. Data from *in vitro* work was correlated with work of other investigators to suggest two sites to be responsible for the effects measured *in vivo*. Antimyosin injected intravenously and auto-

antibodies induced by the injections of myosin localize at one site on the myosin or actomyosin of the myofilaments and bring about impairment of electrical conduction of the sarcolemma or death of the organism. The ergastoplasm and sarcolemma form the second site where antibodies localize to impair the electrical conductive capacity of the sarcolemma. These antibodies are probably specific for a myosin-nucleoprotein intermediate which arises from the nucleus and is found in the microsomal and soluble proteins fractions and the solubilized mitochondrial fraction. *In vitro* serological data indicate a similar arrangement for actin but no *in vivo* effects could be distinguished. Antimitochondrial bodies localize on mitochondria *in vivo* but do not affect the organisms' physiology. It is suggested that antibodies localize on the exterior of the mitochondrial limiting structure and do not inhibit metabolism.

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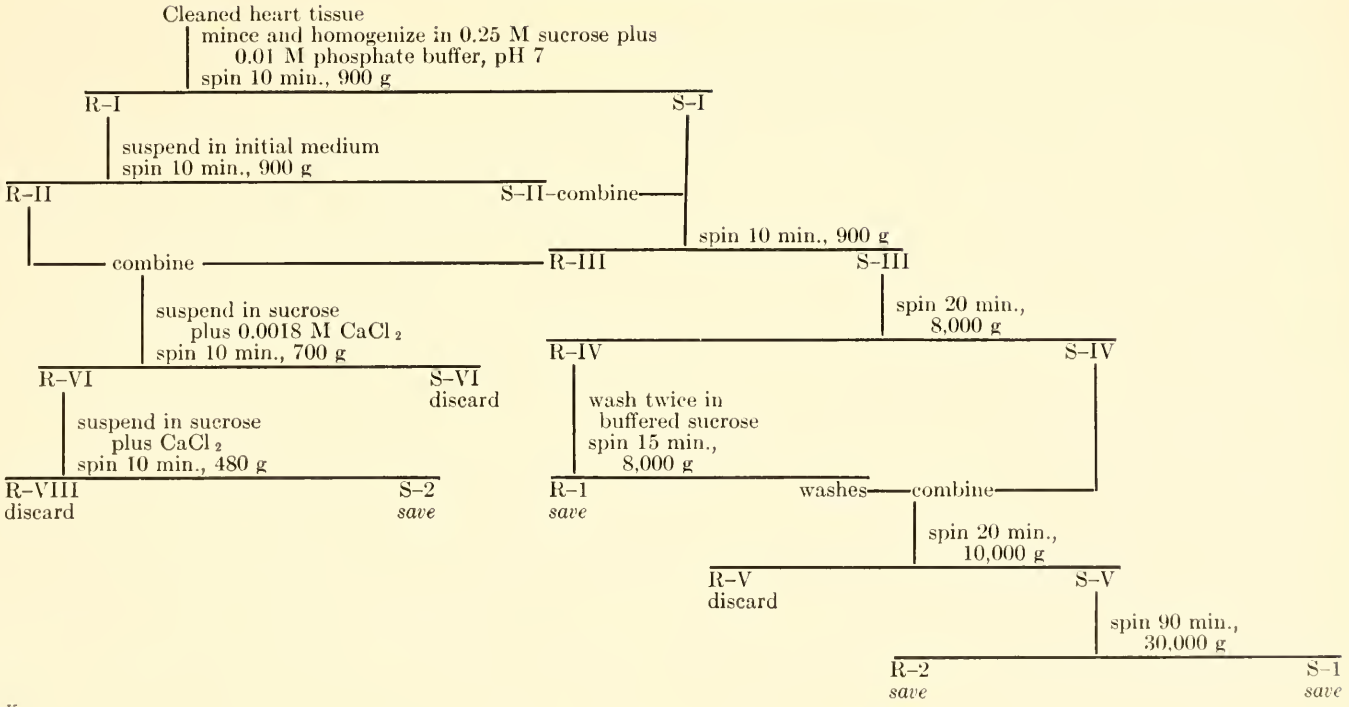
FIGURE 1.—Scheme for fractionation of chicken hearts.



KEY:

S-I, S-II, S-III, S-IV, S-V and S-VI are supernatants centrifuged or discarded as noted.
R-I, R-II, R-III, R-IV, R-V, R-VI and R-VIII are residues resuspended or discarded as noted.
R-1 is fraction which contained greatest concentration of mitochondria.
R-2 is fraction which contained greatest concentration of microsomes.
S-1 is fraction which contained all soluble proteins and a minimal amount of particulate matter.
S-2 is fraction which contained a great concentration of nuclei and a minimal amount of other particulate matter or soluble protein.

FIGURE 2.—Scheme for the extraction of myosin and actin.

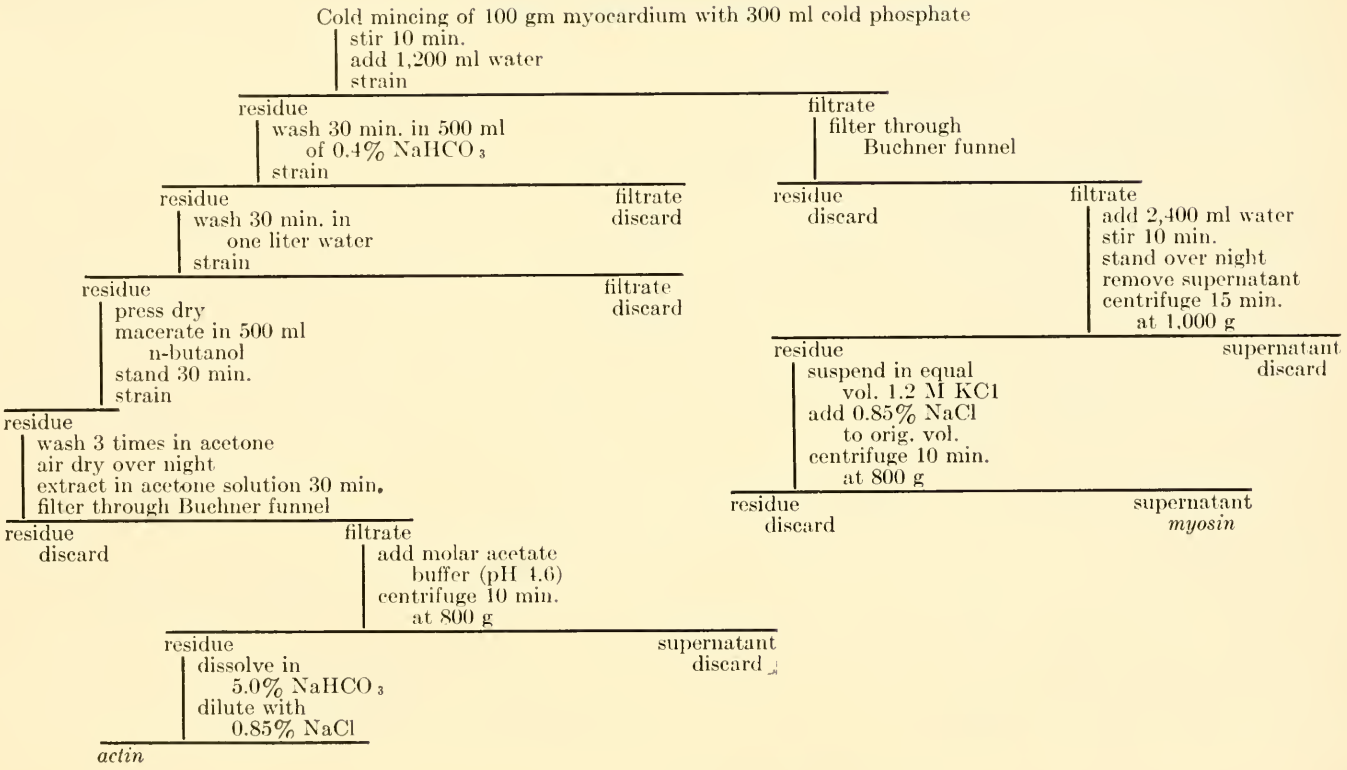
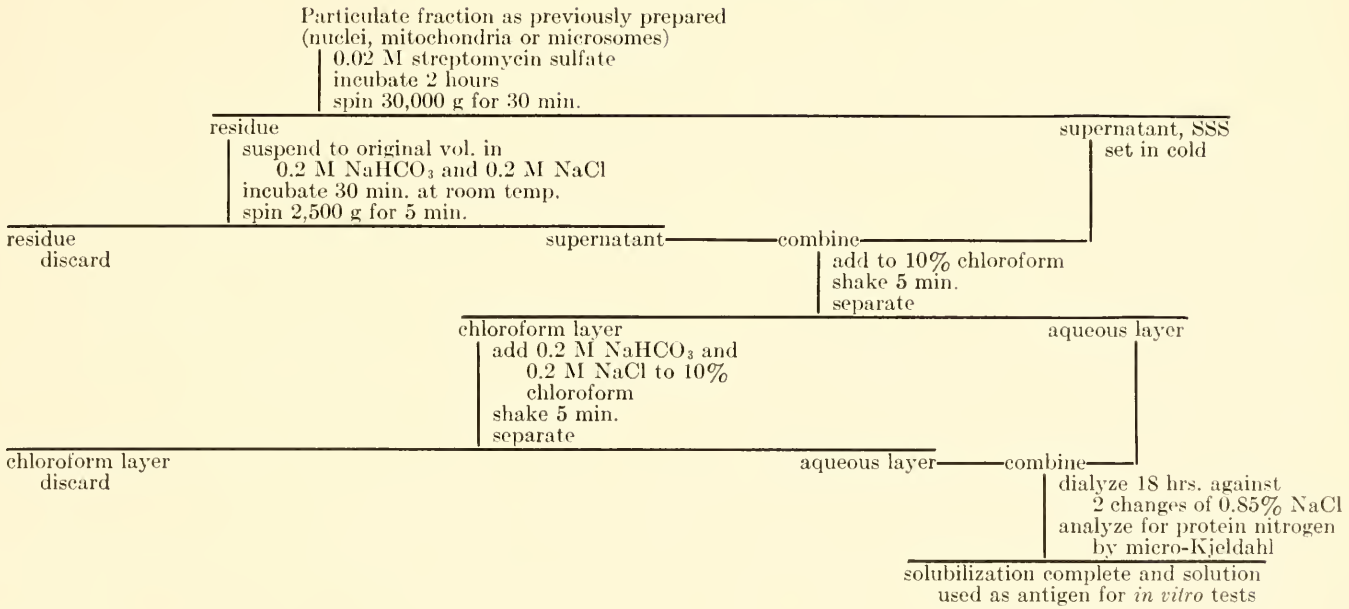


FIGURE 3.—Scheme for the chemical solubilization of particulate fractions.



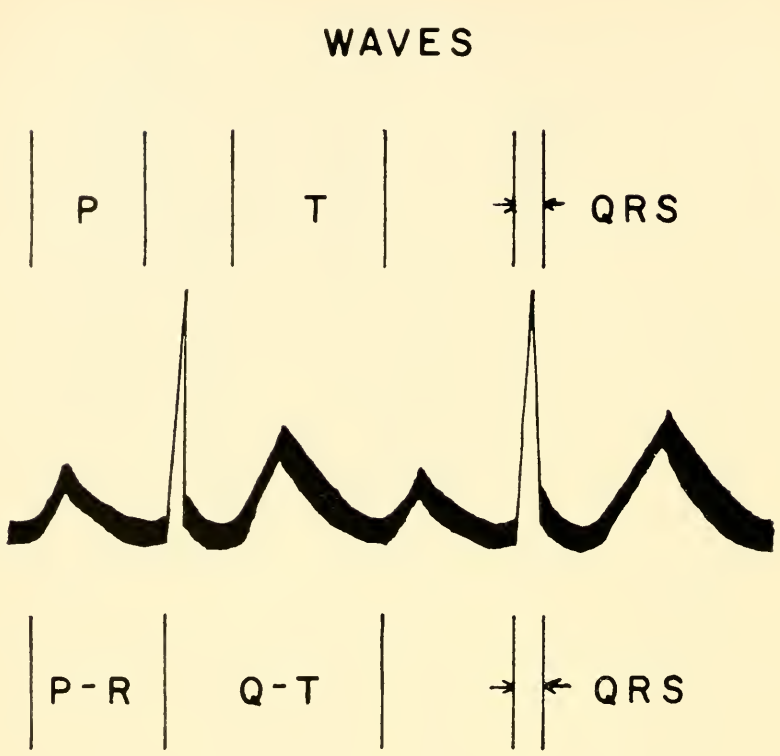


FIGURE 4.—Tracing of the electrical activity through two cardiac cycles.

The electrical waves shown here were recorded at Lead II of an electrocardiogram from a rabbit's heart. Components of one cycle are marked above the tracing and three measurements utilized in ECG analysis are marked below.

TABLE I.—Examples of the injection schedules followed in the production of antisera.

RABBIT	Antigen	Amount	Route*	Notes
VB359.....	Myosin	0.5 ml	S.C.	One part antigen solution plus one part Freund's adjuvant injected as emulsion.
		5.0 ml	I.P.	No adjuvant.
		5.0 ml	I.P.	No adjuvant.
		5.0 ml	I.P.	First partial bleeding. No adjuvant.
		5.0 ml	I.P.	No adjuvant.
		5.0 ml	I.P.	Second partial bleeding. No adjuvant.
		5.0 ml	I.P.	No adjuvant.
		5.0 ml	I.P.	Third and terminal bleeding.
VB1959.....	Microsomes	0.5 ml	S.C.	One part antigen solution plus one part Freund's adjuvant injected as emulsion.
VB2059.....	Soluble proteins			
VB2159.....	Nuclei	4.0 ml	I.P.	One part antigen solution plus one part emulsion oil injected as emulsion.
VB2459.....	Mitochondria			
VB2559.....	Actin	3.0 ml	I.P.	First partial bleeding. No adjuvant.
		3.0 ml	I.P.	No adjuvant.
		3.0 ml	I.P.	Second partial bleeding. No adjuvant.
		3.0 ml	I.P.	No adjuvant.
		**3.0 ml	I.P.	Third partial bleeding. No adjuvant.
		**3.0 ml	I.P.	No adjuvant. Fourth and terminal bleeding.

* S. C. = subcutaneous injection and I. P. = intraperitoneal injection.

** VB1959 and VB2459 received only 1.0 ml of their particular antigen.

TABLE II.—Microscopic observation of fractions from high-speed differential centrifugation.

FRACTION	Cells, Fibers, Large clumps	Small Oval globules*	Methylene blue stain	
			Deep stained, short rods	Light stained, small oval globules
R-VII	+	+	+	+
Nuclear	—	—	+	—
Mitochondrial	—	+	—	+
Microsomal	—	—	—	+
Soluble proteins	—	—	—	—

* Brownian movement was present in all fresh fractions except soluble proteins.

One drop of each fraction was observed unstained as a hanging drop. One drop of each fraction was stained using methylene blue. Magnification was 900 × and 440 ×. The fraction R-VII contains debris obtained as sediment at 480g.

TABLE III.—Ratios of areas under serological curves.

ANTIGENS	Antisera produced against:				
	Nuc	Mit	Mic	Sol	Myo
Reaction measured by quantitative Nessler's:					
Nuclei-particulate	1.0	8.6	1.3	2.8	1.1
Mitochondria-particulate	0.3	1.0	0.2	0.5	0.1
Microsomes-particulate	0.8	6.1	1.0	0.8	0.4
Soluble proteins	0.7	5.8	1.1	1.0	0.6
Myosin	0.6	7.4	1.5	0.9	1.0
Reaction measured by turbidity:					
Nuclei-sonic	1.0	1.3	1.9	.....	1.4
Mitochondria-sonic	0.8	1.0	1.6	0.9	1.3
Microsomes-sonic	0.4	0.6	1.0	0.6	0.9
Soluble proteins	0.8	0.9	1.3	1.0	1.2
Myosin	0.7	0.7	1.1	0.8	1.0

Serological reactions are represented by ratios of the areas under each heterologous curve to that of the homologous curve. All reactions of an antiserum with the five antigens are adjusted to the homologous reaction for which the value is 1.0. The curves are compared only through range of corresponding antigen concentration, that is, 0.1 to 1.0 micrograms of antigen nitrogen.

'Particulate' refers to the preparation of an antigen as it is obtained by differential centrifugation. 'Sonic' refers to a particulate antigen which had been solubilized by 30 minutes of sonic oscillation. The same solutions of soluble proteins fraction and of myosin are used for the quantitative Nessler's and for turbidity measurements.

The data are averaged values obtained with antisera from two or more antisera except for the values of antiactin which are for one antiserum. Abbreviations are as follows: Nuc, nuclear fraction of chicken heart, VB2159 and VB2359; Mit, mitochondrial fraction of chicken heart, VB559, VB5758 and VB2459; Mic, microsomal fraction of chicken heart, VB659, VB5858 and VB1959; Sol, soluble proteins fraction of chicken heart, VB2059 and VB2659; and Myo, myosin from chicken heart, VB5558 and VB359.

TABLE IV.—Agar-plate precipitin reactions of antisera.

ANTISERA PRODUCED BY:	Rabbit number	Antigen						
		Nuc	Mit	Mic	Sol	Myo	Act	ChP
Control sera	IC850	—	—	—	—	—	—	O
Antinuclei	VB459	—	—	—	—	—	—	O
	VB2159	+*	—	—	++*	+*	+	O
	VB2359	+*	—	—	++*	+*	—	—
Antimitochondria	VB559	+	—	—	—	—	—	O
	VB5758	+	—	—	++	—	—	O
	VB2459	—	—	—	—	—	—	O
Antimicrosomes	VB659	—	—	—	—	—	—	O
	VB5858	—	—	—	—	—	—	O
	VB1959	+*	—	—	++*	+*	—	—
Antisoluble proteins	VB2059	—	—	—	—	—	—	—
	VB2659	—	—	—	+	—	—	+
Antimyosin	VB359	+	—	—	++	—	+	O
	VB5558	+*	—	—	+	+*	+	O
Antiactin	VB2259	—	—	—	+	+*	+*	—
	VB2559	+*	—	—	++*	+*	+*	+*

The antigen abbreviations are keyed as follows: Nuc, solubilized nuclear fraction of chicken heart; Mit, solubilized mitochondrial fraction of chicken heart; Mic, solubilized microsomal fraction of chicken heart; Sol, soluble proteins fraction of chicken heart; Myo, myosin from chicken heart; Act, actin from chicken heart; and ChP, chicken plasma. The absence of a reaction zone is denoted by — and the presence of a reaction zone by +. More than one reaction zone is indicated by the appropriate number of + marks. When the comparison was not made, O is used. An asterisk indicates that the reaction zone of the antigen showed partial or complete identity with the reaction zone of another antigen.

TABLE V.—Hatchability of eggs injected intravenously.

INJECTION	Relative hatchability	Ratio
Chicken Ringer's (Romanoff)	1.0	15/28
Control antisera, IC850 and IC1150	0.7	8/20
Antinuclei, VB2159	0.5	5/19
Antinuclei, VB2359	0.3	3/20
Antimicrosomes, VB1959	0.6	6/20
Antimyosin, VB359	0.3	5/30
Antimyosin, VB5558	1.1	6/10
Antimyosin plus antimitochondria, VB5558-VB5758	0.5	4/14
Antiactin, VB2259	0.7	4/10
Antiactin, VB2559	0.6	9/29

Eggs were injected intravenously with 0.2 ml. volume of inoculum after nine to 11 days of incubation. Fraction expresses the number of eggs which hatched to the total number of eggs injected but not infected. Relative hatchability is based on the number of eggs surviving the inoculation of sterile Ringer's saline solution.

TABLE VI.—Statistical analyses of the electrocardiographic measurements.

ECG MEASUREMENTS	Antigens injected	Statistic values				
		N	n	$\bar{x}$ or X	s=	P
Rate bpm.....	All rabbits	20	20	260	15	.....
P-R msec.....	Control	6	6	70	6	.....
	Nuclei	3	3	63	12	>.200
	Mitochondria	3	2	70	4	>.500
	Microsomes	3	2	70	0	>.500
	Soluble proteins	2	1	110	.....	<.005
	Myosin	2	2	60	0	>.050
	Actin	1	.....	80	.....	>.100
QRS msec.....	Control	6	6	20	0	.....
	Nuclei	3	3	37	6	>.001
	Mitochondria	3	2	25	7	>.200
	Microsomes	3	2	35	7	<.001
	Soluble proteins	2	1	30	.....	<.001
	Myosin	2	2	35	7	<.001
	Actin	1	.....	20	.....	>.500
Q-T msec.....	Control	6	6	145	3	.....
	Nuclei	3	3	143	32	>.500
	Mitochondria	3	2	145	7	>.500
	Microsomes	3	2	150	14	>.500
	Soluble proteins	2	1	180	.....	<.001
	Myosin	2	2	130	10	<.005
	Actin	1	.....	140	.....	>.100
Cycle msec.....	Control	6	6	250	13	.....
	Nuclei	3	3	226	31	>.100
	Mitochondria	3	2	235	31	>.200
	Microsomes	3	2	255	7	>.500
	Soluble proteins	2	1	300	.....	<.010
	Myosin	2	2	250	28	>.500
	Actin	1	.....	310	.....	<.005

Measurements from the ECGs included the heart rate in beats per minute (bpm), P-R interval in milliseconds, QRS in msec., and Q-T interval in msec. The number of rabbits (n) used for statistical testing and the total number of rabbits (N) used in experimentation are given. The mean value ($\bar{x}$) of each electrocardiographic measurement and the standard deviation (s) from the mean for each group of injected rabbits are indicated. Where only one rabbit was available, the measured value (X) is given. Probability (P) for a group of injected rabbits being part of the control group was determined using a *t*-distribution table. Some rabbits were rejected from the statistical comparisons because their heart rate was outside 0.001 probability level.

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The Effects of Gibberellic Acid on Diastase, Catalase, and on Germination of Some Common Cultivated Plants

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ABSTRACT: Applications of gibberellic acid below 100 p. p. m. to seeds were noted to cause increases in the maltose content of seven common cultivated plants. A decrease in the catalytic activity of bean plant tissue was found after GA treatment. Included also are general growth changes and germination rates after gibberellin applications.

INTRODUCTION

Recently a group of plant growth regulators, the gibberellins, have been widely used in research. These substances are obtained from cultural filtrates of the fungus *Gibberella fujikuroi* (Saw.) Wr. which is responsible for the "bakanae" disease of rice.

A great number of papers dealing with research findings of gibberellin studies and reviews of the gibberellin literature are available to the reader. In the author's opinion to repeat much of this information would be superfluous. However, the following references are to be consulted for the reader's personal edification, Stowe and Yamaki, (1957) and Stodola (1958).

EXPERIMENTAL PROCEDURE AND RESULTS

Diastase Determinations

Seeds of the following plants were used for the enzyme analysis: *Hordeum vulgare, Avena sativa, Triticum aestivum, Pisum sativum, Secale cereale, Zea Mays* (sweet corn) [1], and *Phaseolus vulgaris* (Bluelake variety No. 93058) [2].

1. Seeds courtesy of Underwood Seed Co., Lawrence, Kan.
2. Seeds courtesy of Rogers Bros. Seed Co., Idaho Falls, Idaho.

Seeds of near equal size were placed in gibberellic acid solutions of 0, 1, 10, 100, and 500 parts per million (p. p. m.) and allowed to soak eight hours. They were then transferred to petri dishes fitted with filter papers and arranged to allow circulation around each seed. The seeds were then covered with another sheet of filter paper to lessen the possibility of microorganism contamination and help maintain the humidity in the dish. The seeds were allowed to germinate 72 hours at room temperature at which time they were dried in a vacuum oven, 36-38° C. for 36 hours. After drying, the seeds were ground to powder fineness using a Waring blender and a mortar and pestle. The ground material was quick frozen at —10° C. and stored until the enzyme determinations were made.

The method used for the diastatic action determination was that of Blish and Sandstedt (1933). This procedure, used in the milling industry for flour analysis, is applicable to germinated seeds with one deviation used by the author. Instead of using five ml. of filtrate as used for flour, one ml. of seed filtrate was used and this brought to a total volume of five ml. by the addition of water. The results of this technique gives one a reading of milligrams of maltose produced from starch in ten grams of ground germinated seeds per one hour's diastasis. These results are listed in table I. From the data in table I, one can note a general maltose increase up to a gibberellic acid-concentration of 100 p. p. m. and then this value drops off or remains somewhat constant.

Catalase Activity

Seeds of *Phaseolus vulgaris* (Bluelake variety, No. 93058) were soaked eight hours in water. They were then placed in seven inch pots filled ⅔ full of sterilized soil and covered with medium-grade sand. Water was added when needed and the photoperiod was extended four hours over that of early February by a bank of fluorescent bulbs kept one foot over the growing plants.

When the plants reached a height of six inches they were thinned to three per pot and treated with gibberellic acid solutions of 0.0, 0.5, 1.0, 10.0, 100.0, and 500.0 p. p. m. as foliar sprays. Three successive treatments followed at 96-hour intervals. Forty-eight hours after the final application of GA, the plants were measured and the leaf and stem tissue harvested. Part of the tissue was frozen at —10° C. to determine whether storage of the tissue affects catalase activity. The remainder of the material was analyzed immediately.

The method for analysis of the catalase activity was that outlined in Loomis and Shull (1939). For the analysis experimentation proved the following proportions of materials most satisfactory. One gram of plant tissue was ground two minutes with one gram of $CaCo_3$ and fifteen ml. of water. The length of time for the maceration is important and must be standardized to assure proper comparisons of catalytic activity. A two and one-half ml. aliquot of the suspension and an equal amount of 4% H_2O_2 were added to the arms of a catalase tube and allowed to react 30 seconds at 30° C. under constant agitation.

Both leaf and stem tissue were analyzed in the same manner. The stem portion used was taken from between the cotyledon attachment and the second node for uniformity. The catalase activity comparisons are listed in table II. Data for the stored material are not present but a definite drop in activity was noted after six week's storage. The over-all changes in size of the bean plants used for the above analyses due to GA treatment are shown in table III.

Seed Germination

That gibberellin affects the germination and sprouting of seeds has been reported by Hayashi (1940), Wittwer and Bucovac (1947), and Helgeson and Green (1957). After noting varying rates of germination of seeds for the determination of diastatic action, tests were designed to more specifically ascertain the effect of gibberellic acid on seed germination.

One hundred seeds each of *Triticum asetivum, Hordeum vulgare, Avena sativa, Secale cereale, Pisum sativum,* and *Zea Mays* were soaked eight hours in GA solutions of 0, 1, 10, 100, and 500 p. p. m. The seeds were transferred to petri dishes prepared in the same manner as in the diastatic action determinations and germinated 72 hours at room temperature.

The variation in the rate of germination is based upon two criteria: (1) a seed was considered germinated if the length of the radicle was at least one cm.; (2) for those seeds considered germinated the average length of the radicle was tabulated. Criterion (1) gives one the percentage germination of the seeds based on actual growth; (2) establishes a quantitative basis upon which comparisons can be made with the change in the GA concentration. See table IV for germination data.

From the data in table IV, one could say that the rate of growth of the seeds is more greatly affected than is the percentage germination, as in some cases the radicle length of the treated seeds is twice that of the control seeds.

The actual effect of gibberellin on seed germination can, in some cases, be questioned. Although the rates of growth are hastened, the final over-all germination percentage in the seeds tested was found to be nearly the same if they were allowed to germinate beyond the 72-hour experimental period.

Discussion

It is well-known that elongation of cells in the stem and leaves of gibberellin-treated plants occurs. Whether this growth is due to an elongation of cells or to increased mitotic activity is an unsettled question. But the evidence presented in other papers (Brian *et al.*, 1954; Kato, 1955; Lang, 1956; Sachs *et al.*, 1959), lends to the idea that both do occur, with cell elongation seemingly being more prevalent.

The mechanism behind the many responses of plants to gibberellin is a problem on which many researchers are now engaged. Many ideas have been postulated as to the pathways utilized by this growth substance. Brian (1958) has attributed gibberellin activity to a neutralization of a growth-inhibiting system in the plant. Reduction of this inhibitor allows normal growth to ensue. Ideas have been put forth attempting to equate the action of gibberellin with that of auxin. The basis for this supposition is the similar manner in which both cause cell elongation. But due to the inactive response of gibberellin to the standard *Avena* coleoptile test (Brian *et al.*, 1955) and its ability to move freely through the plant as opposed to auxin's definite polarity (Stowe and Yamaki, 1957), the gibberellins are not classed as auxins. Another point that serves to separate these two growth hormones is the concentration range in which they best operate. Gibberellin has a greater range in which activity occurs as opposed to the lower, more narrow concentration range of auxin activity.

Work is now in progress that perhaps may hold the key to opening the door of a better understanding of the gibberellins. This work is through genetical studies. B. O. Phinney (1960), by using known single-gene dwarf mutants of maize has presented interesting data on the pathways of the gibberellins.

Research in the action of gibberellin has shown changes occurring in the carbohydrate constituents of treated plants (Hayashi, 1940), (Brian *et al.*, 1954), (Wittwer *et al.*, 1957), and (Hayashi and Murakami, 1958). The data presented in this paper show definite fluctuations in the maltose content of plants treated with GA. Hayashi *et al.* (1953) report decreases in starch and sucrose reserves

in the leaf sheaths of rice. Colorimetric tests by the author during the research for this paper revealed varying starch decreases in the plant preparations after one hour's diastasis.

Previous attempts have been made to give reasons for the fluctuations in the constituents of gibberellin tissues, but with little success. One reason for this is that the responses of plants to gibberellin vary widely from no sensitivity to extreme sensitivity.

No attempt is made in this paper to describe the fluctuations in the carbohydrate material as due to an alteration in a complex metabolic pathway. It can be noted in the data of this paper that the seeds germinated in the lower concentrations of GA display the greatest changes in growth undergone in the 72-hour period. These increases in growth closely correspond to the concentrations in which the increased diastatic action was noted. It would seem reasonable to assume that the increased maltose values found are primarily due to more carbohydrate material present in the tissues as a result of increased growth. Additional evidence for this view is presented by the data for *Zea Mays* in table I. In this, corn allowed to germinate 96 hours displayed substantially larger maltose values than the corn seeds grown 72 hours. The growth of the 96-hour corn displayed a corresponding increase over the 72-hour plants.

The data presented here for the activity of catalase show a decrease over that of the control plants. (See table II.) This supports the findings of Hayashi *et al.* (1956) in rice although Kato (1956) reports slight increases of catalase activity in tissues treated with gibberellin at concentrations of 0.5-1 mg. L. The plants treated for the experimental analysis of this paper were noted to develop varying degrees of chlorosis over that of the control plants, a characteristic of gibberellin-treated plants. If catalase is present to some extent in chloroplasts—Neish (1939) reports such in *Articum* and *Onoclea*, one would expect a decrease in the catalase activity of tissues appearing somewhat blanched.

TABLE I.—Diastatic Action Determinations. Activity is expressed in mg. maltose/10 grams seed/1 hour diastasis.

PLANT	G.A. Conc. (p.p.m.)	Activity
Hordeum Vulgare	0	510
Hordeum Vulgare	1	675
Hordeum Vulgare	10	710
Hordeum Vulgare	100	860
Hordeum Vulgare	500	530
Triticum aestivum	0	575
Triticum aestivum	1	670
Triticum aestivum	10	860
Triticum aestivum	100	570
Triticum aestivum	500	460
Phaseolus vulgaris	0	150
Phaseolus vulgaris	1	130
Phaseolus vulgaris	10	148
Phaseolus vulgaris	100	165
Phaseolus vulgaris	500	130
Pisum sativum	0	360
Pisum sativum	1	360
Pisum sativum	10	348
Pisum sativum	100	364
Pisum sativum	500	84
Avena sativa	0	182
Avena sativa	1	230
Avena sativa	10	292
Avena sativa	100	216
Avena sativa	500	212
Secale cereale	0	740
Secale cereale	1	610
Secale cereale	10	590
Secale cereale	100	680
Secale cereale	500	625
Zea Mays (72 hours)	0	180
Zea Mays (72 hours)	1	194
Zea Mays (72 hours)	10	234
Zea Mays (72 hours)	100	210
Zea Mays (72 hours)	500	191
Zea Mays (96 hours)	0	610
Zea Mays (96 hours)	1	588
Zea Mays (96 hours)	10	690
Zea Mays (96 hours)	100	576
Zea Mays (96 hours)	500	512

TABLE II.—Catalase Activity. The catalytic activity is listed as cc. oxygen liberated from H_2O_2 in 30 seconds.

Phaseolus vulgaris	G.A. Conc. (p.p.m.)	Tissue activity	
		Stem	Leaf
Phaseolus vulgaris	0.0	5.80	42.0
Phaseolus vulgaris	0.5	6.75	38.5
Phaseolus vulgaris	1.0	4.70	32.0
Phaseolus vulgaris	10.0	2.60	28.0
Phaseolus vulgaris	100.0	3.72	25.8
Phaseolus vulgaris	500.0	5.75	31.8

TABLE III.—The effect of gibberellic acid on the growth rate of *Phaseolus vulgaris*. The height of the plant is measured from the soil level to the stem apex.

	Gibberellin concentration (p. p. m.)					
	0	0.5	1	10	100	500
Height (cm.) 12 days	19.6	23.40	25.87	25.00	28.88	28.68
Height (cm.) 21 days	66.85	73.13	74.99	90.47	106.80	92.38

TABLE IV.—Germination studies. The data indicates the percent of seeds germinating at varying concentrations of gibberellic acid and the growth of the radicle in cm. during the 72-hour experimental period.

	Concentration of Gibberellic Acid (p. p. m.)									
	0		1		10		100		500	
	%	cm.	%	cm.	%	cm.	%	cm.	%	cm.
Triticum aestivum	77	2.07	65	2.32	71	2.33	0	0	0	0
Hordeum vulgare	73	1.21	69	1.26	74	1.54	54	1.13	0	0
Secale cereale	71	1.81	62	1.76	64	2.08	39	2.00	0	0
Avena sativa	22	1.27	17	1.69	40	1.28	4	1.08	0	0
Zea Mays	82	1.20	88	1.69	88	2.49	32	1.05	12	1.10
Pisum sativum	84	1.71	74	1.40	90	2.84	8	1.12	6	1.02

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Taeniopteris, Walchia and *Dichophyllum* in the Pennsylvanian System of Kansas [1]

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ABSTRACT: *Taeniopteris, Walchia* and *Dichophyllum* are known only from two localities in the Pennsylvanian of Kansas. They are considered to be representatives of a plant association which grew on higher and better-drained land than the more familiar Pennsylvanian coal-swamp associations. There is no evidence of fossil soil or of fossil roots penetrating the rocks at either locality, and the plant remains were presumably transported to the sites of deposition by water. The presence of *Taeniopteris, Walchia* and *Dichophyllum* has also been used previously to support a theory of fluctuating Pennsylvanian climates in Kansas, but since coal-swamp assemblages occur at other contemporary localities with no admixture of *Taeniopteris, Walchia* and *Dichophyllum*, their occurrence in the Pennsylvanian of Kansas cannot reflect general climatic conditions.

INTRODUCTION

Many leaves referable to *Taeniopteris* have recently been discovered in the Ireland Sandstone member of the Lawrence Shale (Pennsylvanian System) at Baldwin, Kansas. These are associated with a few specimens of *Walchia*, a specimen of *Dichophyllum* and an assemblage of typical Pennsylvanian swamp plants (Cridland and Morris, 1960). The presence of *Taeniopteris, Walchia* and *Dichophyllum* at Baldwin, at once recalls a similar association of these three genera in the Pennsylvanian System of Kansas which was reported by Elias (1932, 1936) and Moore *et al.* (1936), from the Rock Lake Shale member of the Stanton Limestone. Extensive

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recent studies of the Kansas Pennsylvanian plant fossils (Cridland, Morris, and Baxter, 1963) have revealed no further occurrences of these genera.

Dichophyllum is of interest since it is known only from these two localities. When *Taeniopteris* and *Walchia* were found at Garnett some paleobotanists (Jongmans and Gothan, 1934, p. 39; D. White, see Moore *et al.*, 1936, pp. 2 and 12) suggested that the rocks in which they occurred, were of Permian age, and as recently as 1958 Bode (p. 235) has claimed that it is doubtful that the Garnett beds carrying these plants are correctly placed in the Lansing Group. However, careful study (Moore *et al.*, 1936; Ball, 1959) has shown beyond any doubt that the fossils from Garnett occur in the Rock Lake Shale member of the Stanton Limestone, which is correctly placed in the Lansing Group (Missourian Stage) of the Pennsylvanian System of Kansas. Although *Taeniopteris* and *Walchia* are found much more commonly in geological systems younger than the Pennsylvanian, these two genera have been reported from some Upper Carboniferous and Pennsylvanian rocks (Darrah, 1935, 1936; Florin, 1938-1945; Arnold, 1941; Read, 1947). The Permian index fossil, *Callipteris conferta,* has not been found in the Stanton Limestone. Jongmans' and Gothan's (1934) claim for the presence of a species of *Callipteris* at Garnett is an error (Moore *et al.*, 1936, p. 16; Andrews, 1941, p. 376).

Dr. J. M. Jewett and Mr. S. M. Ball assure us that there is no doubt that the fossils from Baldwin come from rocks which are correctly placed in the Ireland Sandstone member of the Lawrence Shale, a well-known Pennsylvanian formation (Moore, 1949; Moore *et al.*, 1951) for which no consideration of Permian age can be entertained. The Pennsylvanian System of Kansas is sufficiently well known (Moore, 1949; Moore *et al.*, 1951; Jewett, 1959) to exclude any possibility of stratigraphic equivalence between the Garnett and Baldwin localities. According to Jewett (1959), in northern Kansas the Rock Lake Shale member of the Stanton Limestone (Garnett locality) lies approximately 100-150 feet below the Ireland Sandstone member of the Lawrence Shale (Baldwin locality).

Elias explained the presence of *Taeniopteris, Walchia* and *Dichophyllum* in the Rock Lake Shale at Garnett by postulating that these plants were representatives of a dry soil or high land association (Moore *et al.*, 1936, pp. 20-22), and he also claimed that the succession of plant assemblages in the late Paleozoic of Kansas reflects cyclic climatic changes (Elias, 1936; Moore *et al.*, 1936, p. 22), with generally drier climatic conditions existing when the Garnett

plants were deposited. The discovery of *Taeniopteris, Walchia* and *Dichophyllum* in the Ireland Sandstone member of the Lawrence Shale is of particular interest, since the Lawrence Shale and its Ireland Sandstone member have abundant plant fossils at many localities. Thus comparisons can be made between assemblages from these localities. In contrast, the Garnett locality is the only place where plant fossils are known in abundance from the Rock Lake Shale, and no other fossil plants are known from the Stanton Limestone. Comparisons of the plant fossils from the different localities in the Lawrence Shale and its Ireland Sandstone member shows quite definitely that while *Taeniopteris, Walchia* and *Dichophyllum* flourished in Kansas, there were contemporaneous associations lacking these genera. This irregular distribution of *Taeniopteris, Walchia* and *Dichophyllum* can be explained by Elias's theory that these genera were members of a plant association growing on higher and hence better-drained ground than that which supported the more usual Pennsylvanian coal swamp plants. This same irregular distribution leads us to doubt the second part of Elias's theory, which postulates over-all cyclic climatic changes during the Pennsylvanian Period in Kansas.

The manner in which *Taeniopteris, Walchia* and *Dichophyllum* were deposited is still not entirely clear. Peabody (1952) has presented a hypothesis that the Rock Lake Shale at Garnett was deposited in a lagoon into which the remains of terrestrial plants and animals drifted and were fossilized. He suggested this because: *i*) inarticulate brachiopods referable to *Lingula* and pelecypods referable to *Sedgwickia* and *Myalina* are present in abundance, and Newell (Moore *et al.*, 1936, p. 28) considers that these indicate brackish or otherwise abnormal marine conditions; *ii*) the Rock Lake Shale is very fine-grained; *iii*) deposition of shale was interrupted by the deposition of a highly lenticular but locally absent sandstone (Newell, in Moore *et al.*, 1936) which in Peabody's (1952) view represents the shoreward advance of a barrier bar; and *iv*) terrestrial plants and animals are associated with marine invertebrates (Peabody, 1952, 1958). The presence of barrier reefs and lagoons in the Stanton Limestone is also supported by an independent study of this formation in southeastern Kansas (Wilson, 1957). At Garnett, Peabody (1952, 1958) suggests that terrestrial and fluviatile organisms were rafted into the lagoon by a slowly-flowing river. However, a lagoon adjacent to the growth site is not essential for the occurrence of *Taeniopteris, Walchia* and *Di-*

chophyllum, since at Baldwin no marine fossils or other evidence of marine sedimentation have been recognized in the Ireland Sandstone, and there is no reason to believe that a lagoon existed.

THE FOSSIL ASSEMBLAGES FROM THE GARNETT AND BALDWIN LOCALITIES

a) Garnett

At the Garnett locality the plant fossils occur associated with animal fossils in the lower and middle parts of the Rock Lake Shale, in about three feet of fine-grained, whitish shale with intercalated shaly limestone (Moore *et al.*, 1936). A list of plants occurring here was published by Elias (Moore *et al.*, 1936), but since this list represents preliminary identifications and includes a number of doubtful designations and unvalid new names (Baxter and Hartman, 1954), and since a few later workers (Florin, 1938-1945; Andrews, 1941; Baxter and Hartman, 1954) have made contributions to the study of the Garnett plants, we present a reappraisal of the Garnett plant assemblage. Unfortunately, we have only been able to locate and re-examine a few of the specimens cited in Elias's (Moore *et al.*, 1936) list. Most of Elias's plants were lost before the Kansas University fossil plant collection passed to the care of the Botany Department. Our knowledge of the Garnett plants is gained mainly from examination of recent extensive collections curated in the Botany Department, the Geology Department and the Natural History Museum at the University of Kansas; the Henry Shaw School of Botany, Washington University, St. Louis, and from recent collections we have made in a roadside ditch (center south line, section 32, T. 19 S., R. 19 E., Anderson county).

The plant fossils are mainly coniferous remains referable to *Lebachia garnettensis* Florin, *Lebachia* being an organ-genus based on specimens previously assigned to the form-genus *Walchia* (Florin, 1940, p. 244-363). Other coniferous remains are *Walchia schneideri* Zeiller and isolated cones of the genus *Walchianthus.* Florin (1940) also reports female cone scales referable to *Gomphostrobus bifidus* (Geneitz) Zeiller. The conifers reported by Elias (Moore *et al.*, 1936) as *Dicranophyllum? garnettensis and ?Lecrosia* have been placed in *Lebachia garnettensis* and *Walchia schneideri* by Florin (1938-1945). *Dichophyllum moorei* Elias ex Baxter and Hartman (1954), an impressive but problematical leaf, which as Elias (Moore *et al.*, 1936) points out, is strikingly similar to *Mauerites gracilis* Zalessky (1933), is next in abundance, and a small seed, *Diceratosperma carpenteriana* Andrews (1941), is com-

mon. The affinities of both *Dichophyllum* and *Diceratosperma* are unknown and the suggestions of ginkgoalean affinity for *Dichophyllum moorei* (Andrews, 1941; Baxter and Hartman, 1954), which are based principally upon the external form of the leaf, and the suggestion that *Diceratosperma carpenteriana* was borne on *Taeniopteris* (Cridland and Morris, 1960) are no more than speculations.

Taeniopteris leaves are known from Garnett, but all the specimens we have seen are fragmentary and insufficiently preserved for specific identification. The genus *Spermopteris*, which was established by Cridland and Morris (1960) for species with the characters of *Taeniopteris* but bearing rows of seeds on their abaxial surface, is represented by one specimen in the Botany Department collection at Kansas University, but likewise this cannot be specifically determined. In addition to the plants mentioned above, fern-like foliage and other typical coal swamp plants play a very subordinate role and occur mainly as indeterminable fragments. From the material we have seen, we have been able to identify specimens of *Annularia galioides* (Lindley and Hutton) Kidston, *Cordaites* sp., *Lepidodendron* sp., *Lepidophyllum* sp., *Neuropteris attenuata* Lindley and Hutton, *Neuropteris* sp. and *Pterispermostrobus* sp. *Alethopteris* sp. can be recognized from Moore *et al.* (1936, figures 6.8, 6.9, 8.5). The anatomy of an isolated piece of fusinized coniferous wood has also been studied by Baxter and Hartman (1954) who suggest it belongs to *Dichophyllum moorei*. Spores referable to *Florinites* are abundant in the Rock Lake Shale at Garnett, and it is probable that most of these were shed by *Lebachia garnettensis*.

The plant fossils from Garnett occur in association with invertebrate and vertebrate animal fossils. The invertebrates are mainly brachiopods, pelecypods, bryozoans and fusulinids (Newell, in Moore *et al.*, 1936; Elias, 1937). Several arthropods also occur. One of these is a scorpion belonging to the genus *Garnettius* (Petrunkevitch, 1953), while the rest are cockroaches (Peabody, 1952) and a member of the extinct order Megasecoptera (Carpenter, 1933). Besides these a cup coral and crinoid columnals were reported by Peabody (1952). The vertebrate remains known from this locality are coelacanth fish (Hibbard, 1933), an aquatic fish-like amphibian (Eaton and Stewart, 1960), the extensively studied agile and terrestrial reptile, *Petrolacosaurus kansensis* Lane (Peabody, 1952), and an anterior thoracic vertebra of an edaphosaur (Peabody, 1957).

With the exception of outcrops containing small fragments of fusain, which presumably drifted out to sea, there is only one other

outcrop of Rock Lake Shale known to contain plant fossils. This is in Johnson county, Kansas (center south line, section 24, T. 13 S., R. 21 E.) where very fragmentary and poorly-preserved plant fossils occur in association with marine invertebrates in a shale of similar lithology to that exposed at Garnett. Enough can be seen of these plant fossils to demonstrate that they are predominantly remains of fern-like foliage and that there are no fragments of *Taeniopteris, Walchia* and *Dichophyllum.*

b) *Baldwin*

At Baldwin the Ireland Sandstone is a silty shale, and the plant fossils occur about six feet below its erosional surface. Although there is a similarity to the Garnett locality in the presence of *Taeniopteris, Walchia* and *Dichophyllum,* the relative abundance of the different types of plant fossils at the Baldwin and Garnett

BALDWIN

Taeniopteris > swamp plants > *Walchia* > *Dichophyllum moorei*

GARNETT

Walchia > *Dichophyllum moorei* > *Taeniopteris* > swamp plants

FIGURE 1.—Relative frequency of the plant fossils occurring at Baldwin and Garnett.

localities is somewhat different (figure 1). Among the plants occurring at Baldwin (Cridland and Morris, 1960) *Spermopteris coriacea* predominates. In addition, there is an assemblage of Pennsylvanian swamp plants referable to the genera *Calamites, Annularia, Asterophyllites, Ptychocarpus, Neuropteris, Odontopteris, Sphenopteris, ?Schizopteris, Cordaites,* and *Artisia,* and there are a few specimens of *Walchia schneideri* Zeiller, *Walchia* sp. and one specimen of *Dichophyllum moorei* (Table 1, column 11). We have been unable to obtain microfossils from the Ireland Sandstone at the Baldwin locality; this negative result has also been obtained by Dr. R. M. Kosanke (personal communication).

The Ireland Sandstone, the lowermost named member of the Lawrence Shale, is predominantly a tan, medium to fine-grained sandstone which is massive and in part cross-bedded (Moore *et al.,* 1951). It contains both marine and non-marine fossils, but its stratigraphy is very complex and its distribution is imperfectly known. The upper boundary of the Ireland Sandstone is somewhat indefinite because sandy shales and thin-bedded sandstones occur in the upper part of the Lawrence Shale. According to Bow-

sher and Jewett (1943, figure 8) the Ireland Sandstone is in part a facies of the Lawrence Shale. Also, with the exception of the plant assemblage at Baldwin, the plant assemblages in the Lawrence Shale and its Ireland Sandstone member are essentially similar, and for the purposes of discussion we regard them as being of the same age. Comparison of the fossil plants known from the Lawrence Shale and the Ireland Sandstone member in Kansas is made in the form of a table (Table 1) which shows clearly that coal swamp vegetation, without a single fossil referable to *Taeniopteris, Walchia,* or *Dichophyllum* existed in other regions at the same time as the assemblage collected at Baldwin.

DISCUSSION

Evidence suggesting that the Garnett plants lived under dry edaphic conditions was presented by Elias (Moore *et al.*, 1936; Elias, 1936). He considered the scarcity of pteridophytes, the presence of seed-bearing pteridosperms and conifers and the reduced foliage of many of the plants reflected a dry environment. While it is true that most of the Garnett plants probably bore seeds, seed-bearing plants were as abundant, if not more abundant, than pteridophytes in normal Pennsylvanian coal swamps. The validity of Elias's observations on the reduction of foliage of the non-coniferous Garnett plants is equivocal. Some of the foliage may be genuinely reduced (we have not seen abundant enough material to be certain), but *Annularia galioides* which Elias cites as one example of a plant with reduced foliage also occurs in normal plant deposits of Pennsylvanian age (Abbott, 1958, pp. 312-313) where swamp-like conditions undoubtedly existed. A much more convincing argument for believing that the *Taeniopteris, Walchia* and *Dichophyllum* association grew under drier conditions than swamp plants, can be made from the existence of abundant *Taeniopteris* and coniferous plants in deposits of Permian age (*e. g.*, Göppert, 1865-66; Seward, 1933; Georgi, 1955) where there is clear geological evidence, in the form of redbeds deposited in arid conditions, desert sandstones and anhydrite rocks, that in some cases fairly widespread arid climates existed. Both *Taeniopteris* and *Walchia* are common in the Sumner Group of the Permian of Kansas (Sellards, 1901, 1908) at about the position redbeds and anhydrite rocks begin to appear. We make it specifically clear that only those redbeds associated with impressive amounts of anhydrite rocks, or with aeolian sandstones, are supposed to have formed under dry conditions. Other origins of redbeds which are not associated with such rocks

are adequately discussed by Dunbar and Rodgers (1957, pp. 209-218) and many other geological texts. Additional evidence that *Taeniopteris* grew in areas away from coal swamps is provided by Němejc's (1928) study of the Czechoslovakian coal basins. This was the first of a series of discoveries of supposedly Permian plants in Stephanian rocks of the Czechoslovakian coalfields, which have recently been summarized by Havlena (1960). At several localities fragmentary remains of characteristically Permian plants occur in Stephanian rocks. They are not associated with fossil soils and presumably are representatives of plant associations which grew on higher and drier ground, and were subsequently transported to the site of deposition. Remains of *Taeniopteris* and *Walchia* occur in these rocks, as well as *Sphenopteris germanica* and leaves of cordaites assignable to the *Poacordaites* subsection of the genus *Cordaites.* In rocks which are of Stephanian C age several species of *Callipteris* occur, including the Permian index fossil, *Callipteris conferta.* It thus appears that *C. conferta* should only be used to assert Permian age where it occurs in abundance in deposits which are definitely autochthonous.

Independent studies of Permian plants by Gothan and Gimm-Elgersburg (1930) have also led to the recognition of a distinct plant association believed to have flourished under drier edaphic conditions than the contemporaneous swamp plants. In the Rotliegenden of Thüringen, three types of plant assemblages can be differentiated. Above coal seams, the plant remains are predominantly pecopterids, accompanied by *Odontopteris, Calamites, Sphenophyllum* and *Ilfeldia jejunata,* a taeniopterid genus probably belonging to a group of plants that differs from the taeniopterid genus, *Spermopteris* (Cridland and Morris, 1960). Plant associations dominated by callipterids and *Walchia* also occur, but these are never associated with coal seams. These fossils are evidently allochthonous, and Gothan and Gimm-Elgersburg suggest that they have been swept in from higher and drier ground. A third type of plant association recognized by Gothan and Gimm-Elgersburg consists of a mixture of plants from the two types of associations. This third type of association likewise does not occur immediately above coal seams, and is also considered allochthonous.

The possibility that conifers were conspicuous elements of Carboniferous upland vegetation has also been suggested by Chaloner (1958), based upon the work of Neves (1958) who studied the spore contents of a coal and its associated shales. Neves found a

high proportion of *Florinites* in the marine shale and a low proportion in the associated coal and non-marine shale and pointed out that this is the case in other similar Carboniferous deposits. According to Chaloner the spores in the marine shale represent the spore rain from vegetation that grew in uplands away from the swamps, while spores of swamp plants are predominately represented in the coal and non-marine shale. *Florinites* is known to have been shed both by conifers and cordaitean plants, but Chaloner did not assign specific dispersed spores to the appropriate parent plants. If cordaitean plants were members of this upland association, they possibly belonged to the *Poacordaites* subsection of the genus *Cordaites.* Plants referable to this subsection are known to have flourished in the Permian (Gothan and Weyland, 1954, p. 276; Havlena, 1960), and were probably capable of existing under drier edaphic conditions than swamp plants.

Since coal swamp plants existed at the same time as *Taeniopteris, Walchia* and *Dichophyllum,* Elias's (Moore *et al.,* 1936, pp. 20-22) suggestion that the dry land association flourished on higher and hence better-drained ground, than the coal swamp plants, is quite credible, and presents a suitable explanation for the occurrence of both the Garnett and the Baldwin fossil assemblages. The relief of the regions in question need only have been of the order of 20-30 feet, *i. e.,* the order of magnitude which is responsible for the profound differences of the floras of river bottoms and adjacent prairies in present-day Kansas. Our conception of an idealized profile of a Pennsylvanian landscape in Kansas is shown in figure 2.

Perhaps the remains of upland organisms at both these localities were carried to the lowlands by slowly-flowing streams where they were subsequently fossilized. Peabody (1952) suggests the existence of such a stream at the Garnett locality, which carried the fossils from adjacent land. This view of deposition is the most tenable, for at neither the Garnett nor the Baldwin locality, is there any evidence of fossil soil or of fossil roots penetrating the rocks. No case can be made for the deposition of the plant fossils at the growth site, and they were evidently transported to the deposition site. It is also possible that *Taeniopteris, Walchia* and *Dichophyllum* grew on elevated hammocks in coal swamps, natural levees, or were perhaps fossilized when higher land was inundated by the sea. It may well be that an adequate explanation of the mode of deposition of these fossils will not be forthcoming until more detailed geological observations have been made at these localities.

In his discussion of the Garnett plants Elias (Moore *et al.*, 1936; Elias, 1936) also favored a view of over-all climatic changes during the Pennsylvanian Period in Kansas. Elias's view is that in the upper part of the Desmoinesian Stage of Kansas the plants known are chiefly ferns, pteridosperms, sphenophylls, lycopods and cordaites. Later, in the Missourian Stage, plants reflecting a drier climate, *Walchia* and *Cordaites*, predominate, while in the Virgilian Stage there is a return to a wetter climate with *Walchia* disappearing, *Cordaites* becoming rare and the abundance of ferns, pteridosperms, sphenophylls, calamites and lycopods increasing. Towards the end of the Virgilian Stage it became drier again and culminated in dry conditions in the Kansas Permian.

The plant assemblages upon which Elias (Moore *et al.*, 1936; Elias, 1936) based these views were only imperfectly known at the time. For example (based on recent collections by Dr. H. A. Ireland), Elias's (1936) plant assemblage number 7, which he believed reflected dry climatic conditions (Bonner Springs Shale, cement quarry 1½ miles east of Bonner Springs, Wyandotte County) also contains abundant *Neuropteris ovata* Hoffman, *Cyclopteris fimbriata* Lesquereux, *Acitheca polymorpha* Brongniart, and some *Annularia sphenophylloides* (Zenker) Gutbier, besides the fragments of *Cordaites* leaves he reports. Certainly not enough information on the relative abundance of the various plants at each locality was published to support Elias's (1936, p. 964; Moore *et al.*, 1936, p. 6) graphical representation of changing climates. In addition cordaitean remains are found so commonly overlying coal seams we cannot accept Elias's view that their presence can be readily correlated with dry climatic conditions. Also, there is no evidence of the existence of the *Poacordaites* subsection of the genus *Cordaites* in the Kansas Pennsylvanian. It is only specimens referable to this subsection of the genus, which occur commonly in Permian rocks (Gothan and Weyland, 1954, p. 276; Havlena, 1960), that can reasonably be taken as indicators of a dry environment.

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FIGURE 2.—Idealized profile of an Upper Pennsylvanian landscape in Kansas. To the right of the figure there is a lowland coal swamp community composed of *Cordaites* (C), *Calamites* (Ca), *Lepidodendron* (L), ferns and pteridosperms (F) and *Sigillaria* (S). To the left of the figure there is a community of plants growing on slightly higher, hence better drained and drier, soil. This community contains *Dichophyllum* (D), *Taeniopteris* (T) and *Walchia* (W).

TABLE 1.—Fossil plants known from the Lawrence Shale in Kansas. Each locality is represented by a column numbered at the top and the localities to which these numbers refer are shown in Table 2. Based upon specimens in the Botany and Geology Department collections at the University of Kansas.

	Lawrence shale								Ireland ss.		
	Locality number										
	1	2	3	4	5	6	7	8	9	10	11
LYCOPODS:											
Lepidodendron sp.						X					
Lycopod cones			X		X						
Lycopod leaves			X		X						
Sigillaria sp.									X		
S. brardii Brongn.		X	X		X						
ARTICULATES:											
Annularia cf. *asteris* Bell											X
A. mucronata Schenk		X	X		X		X	X			
A. vernensis (Arn.) Abbott											X
Articulate cones			X		X						X
Asterophyllites equisetiformis (Schloth.) Brongn.		X			X						
A. longifolius (Stbg.) Brongn.		X									X
Calamites sp.									X		
C. cistii Brongn.											X
Sphenophyllum oblongifolium (Ger. & Kaul.) Ung.		X	X								
FERNS, PTERIDOSPERMS AND OTHER FOLIAGE:											
Alethopteris grandini (Brongn.) Goepp.		X	X		X				X		
A. serlii Brongn.							X				
A. sullivanti LX.			X								
Alloiopteris sp.									X		
Aphlebia sp.		X				X					
Asterotheca arborescens (Schloth.) Stur.	X	X	X		X						
A. cf. *hemiteloides* (Brongn.) Grand'Eury		X									
A. cf. *miltoni* (Art.) Zeill.								X			
Caulopteris sp.									X		
Cyclopteris sp.									X		
Dichophyllum moorei Baxter & Hartman											X
Dicksonites pluckenetii Schloth		X									
Linopteris cf. *neuropteroides* (Gut.) Potonie									X		
Mariopteris sp.								X			

Neuropteris sp.											X
N. ovata Hoff.		X		X				X	X	X	
N. scheuchzeri Hoff.	X	X	X							X	
Odontopteris sp.				X					X	X	
O. excelsa Sellards											X
Acitheca polymorpha Brongn.		X									
P. candolliana Brongn.		X	X	X	X			X			
P. feminaeformis Schloth.		X							X		
Ptychocarpus unitus (Brongn.) Zeill.					X						
Spermopteris coriacea (Göppert) Cridland & Morris											X
?*Schizopteris* sp.											X
Sphenopteris sp.		X									X
S. obtusiloba Brongn.		X							X		
Taeniopteris sp.											X
CORDAITES:											
Artisia sp.											X
Cordaites sp.		X									
C. principalis Germ.											X
Cordaitanthus sp.		X									
Cordaicarpus sp.		X									
CONIFERS:											
Walchia sp.											X
W. schneideri Zeill.											X

TABLE 2.—Localities for the fossils listed in Table 1.

Locality No.

1. Lawrence Shale. Stony Point Hill, southwest of Vinland, Douglas County.
2. Lawrence Shale. Lone Star Lake, SW¼ Sect. 11, T. 14 S., R. 18 E., Douglas County.
3. Lawrence Shale. Kansas University campus, Lawrence, Douglas County.
4. Lawrence Shale. Junction of Ohio Street and 14th Street, Lawrence, Douglas County.
5. Lawrence Shale. East side of the dam at Tonganoxie Lake, four miles northwest of Tonganoxie, Leavenworth County.
6. Lawrence Shale. Nine miles south of Kanwaka, Douglas County.
7. Lawrence Shale. Pleasant Grove, seven miles south of Lawrence, Douglas County.
8. Lawrence Shale. Four miles south of Pomona, Franklin County.
9. Lawrence Shale, Ireland Sandstone member. Baldwin, Douglas County.
10. Lawrence Shale, Ireland Sandstone member. Near Baldwin, Douglas County. Middle of west line NW¼ Sect. 28, T. 14 S., R. 20 E.
11. Lawrence Shale, Ireland Sandstone member. Baker University, Baldwin, Kansas.

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Taxonomic and Ecological Notes on the Salamander, *Plethodon welleri*

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ABSTRACT: The pigmentation of living *Plethodon welleri ventromaculatus* and that of additional museum specimens support the distinction between this form and *P. w. welleri,* but do not add any fundamental differences. Living specimens did not show any special juvenile pigmentation, nor the suggestion of a dorsal band which appears in some preserved specimens.

A new locality for *P. welleri* in Unicoi Co., Tennessee, is at the low altitude of 2300-2400 feet. The hemlock-yellow birch-*Rhododendron maximum* forest of this valley locality differs somewhat from previously described habitats, as does another collecting site near the top of Grandfather Mountain. Local weather conditions during different seasons indicate part of the range of conditions in which *P. welleri* appears at the surface under various shelters. Some quantitative data span 8-20° C. substratum temperatures, 22-24½% free water in the substratum, 10½-15% organic matter index, and 87-95% relative humidity values partly under the shelter object. Similar values were obtained for three *P. yonahlossee.* An association with talus is compared to one in *P. dorsalis.* Previously unreported salamander associates of *P. welleri* are *P. glutinosus* and *P. yonahlossee, Desmognathus monticola* and *D. quadramaculatus,* and *Diemictylus v. viridescens.*

Food items from nine *P. welleri* are listed. The items suggest the preliminary hypotheses that smaller prey are taken than by larger *Plethodon* species, that arachnids may form a greater percentage of the diet than in *P. cinereus* and that more of the food comes from a sub-forest-floor stratum.

Males collected in spring and fall contained sperm in the vasa deferentia, indicating breeding activity, but summer males did not. No evidence was found for geographical variation in male secondary sex characters, but their development does vary with the season (being better developed in spring and fall), and with size and age. No seasonal differences were noted in the female material, but the shape and pigmentation of the vent also change with age. Size-frequency groupings suggest a yearling group of 21-23 mm. body length and a second year group of 26-27 mm. and perhaps larger. Data indicate that

males mature in the fall at about 30 mm., and usually at three years of age, and suggest that most spring females with enlarging ova exceed 35 mm. and are over three years old.

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TAXONOMIC OBSERVATIONS

P. welleri ventromaculatus was described on the basis of preserved material (Thurow, 1956a). Two additional specimens of this subspecies were collected six miles northeast of Erwin, Tennessee, by road, near Highway 107, in Unicoi Co., on September 16, 1954, and three more on July 31, 1958.

Plates I and II show dorsal and ventral aspects of one of these specimens, in life, and may be compared with figure 79 of Bishop's Handbook of Salamanders (1943) which similarly illustrates *P. w. welleri*. Plate II shows that the light belly spots diagnostic of the subspecies are real spots, with iridophores as well as gaps in the underlying melanophore bed. These spots are white. The color and distribution of iridophores change, roughly at a line connecting the dorsal edges of the two limb insertions. The dorsal frosting is a rich reddish copper in life. The same type of pigment appears on the iris. This color did not appear to change with the angle of

incident light, as do the dorsal spots of some *P. glutinosus*. The "dull golden" of Bishop (1943) or "greenish-bronze" of Walker (1931) suggested a possible subspecific difference. However, an examination of 12 living *P. w. welleri* collected from the top of its restricted range on Grandfather Mountain on April 30, 1960, casts doubt on the diagnostic value of any slight differences in dorsal pigmentation. Five of the 12 were coppery and the others golden. Again the flank iridophores shift to a white or lighter shade, but in these specimens the change appears to be more related to the angle of incident light. The pigment layer appears golden or coppery if held at right angles to the eye, but if held parallel it appears silvery. These specimens (hereinafter often referred to as GRT 1639-50) were distinguishable from *P. w. ventromaculatus* in ventral view, however, according to the description of the latter. Eleven of the former had no belly spotting, or only tiny flecks. The twelfth had some definite spotting and ventrolateral melanophore layer gaps anteriorly, but this did not extend to the groin.

Additional museum specimens have been examined since *P. w. ventromaculatus* was described: Grandfather Mountain, University of Michigan Museum of Zoology (UMMZ) 7185 (2), 75507 (33), and 109145 (7); and Whitetop Mountain, in Virginia, UMMZ 75511 (3), and 109144 (3). These specimens could be subspecifically identified at a glance while in the bottles. More United States National Museum (USNM) specimens (124421-9, from Mt. Rogers, Virginia) and two additional Whitetop Mountain specimens among the 1954 class collections at the Mountain Lake Biological Station were also identified without difficulty.

The smallest living specimen examined (GRT 1644, 20.5 mm. from snout to anterior vent angle) had no dorsal red spots. There appeared to be some red color underneath the melanophore network in two places (at 16X) but this might have been from erythrocytes. Organ (1960) found paravertebral brassy spots on some hatchling *welleri*. He described the spots as formed by coalesced iridophores overlying areas of reduced melanophore pigmentation, and makes no mention of any red pigment. It is desirable to check such brassy or coppery iridophore spots in juvenile *Plethodon* under higher magnification as they sometimes turn out to be a combination of silvery iridophores and small red pigment cells (*e. g.*, in *P. j. jordani* —my own observations at 32X, and those of Reynolds (1959)). At present it can only be said that no red pigment has been observed in *welleri* of any size.

The cryptic dorsal band seen in some preserved *welleri* (Thurow, 1956a: 347) is not visible in live specimens of either subspecies. Organ (1960: 291-2) did not see this band in live embryos and hatchlings, but found it revealed in some of the same individuals after preservation. He states that the brown pigment is merely a thinning of the melanophore layer. He also noted a similarity in dorsal pigmentation between preserved hatchling *welleri* and young *P. yonahlossee*, which agrees with that reported for preserved adults (Thurow, 1956a: 347).

LOCALITY, HABITAT, AND SALAMANDER ASSOCIATES

This additional *P. w. ventromaculatus* locality, between records from Flat Top Mountain and Johnson County, Tennessee, strengthens the hypothesis that this subspecies occupies the Unaka Mountains (in the broad sense), from Flat Top Mountain south of Erwin to Whitetop Mountain and Mt. Rogers in Virginia. The new locality is at the foot of the northwest slope of one ridge, lying mainly east of Erwin, and called Unaka Mountain in the more restricted sense (on topographic maps).

The altitude at which these specimens were collected (approximately 2300-2400 feet) is the lowest elevation from which the species has been recorded, and makes it more likely that a fairly continuous population exists between Flat Top Mountain and Mt. Rogers. Although Unaka Mountain rises above 5,000 feet, the new locality is in the valley, which is a limestone cove.

The environments at this locality and at Grandfather Mountain are different from the spruce-fir forest others have associated with *welleri*. At the foot of the forested northwest slope of Unaka Mountain the trees are mostly hemlock, *Rhododendron maximum*, and yellow birch, with a few scattered tulip, sycamore, and maple. Some of the hemlocks and maples were over two feet in diameter at chest height. The forest floor was a mat of hemlock needles, and fairly clear because of the heavy shade. The area is fairly level, with a small meandering streamlet which usually empties into the main valley stream only a few hundred feet away. The bed of the side streamlet was moist but empty in September, 1954, and partly so in July, 1958. On Grandfather Mountain the 12 specimens were all on or in a fern-and-moss-covered coarse talus in the lee of a cliff. Stunted hemlock and yellow birch grow here, although this is in the spruce-fir zone.

The weather was clear during the visits to Limestone Cove, but a fog and light rain rolled in during the visit to Grandfather Mountain. The substratum temperatures were cooler than the general air temperature at chest height at Limestone Cove, and warmer than the 6° C. chest high temperature on Grandfather Mountain. No salamanders were found at the same locality on Grandfather Mountain in December, 1958, when the air and ground surface temperatures were near freezing by day and considerably below it at night.

The shelters under which all specimens were found, varied, as did the microclimate and other elements of the immediate environment. At Limestone Cove the two *P. welleri* taken in 1954 at the end of a dry summer were each under a short, arm-thick log (one was hemlock), and there was a downward tunnel or passage into the moist cool substrate. Logs sheltering *P. glutinosus* were mostly larger, with more moisture in the wood and underlying substrate, and possibly a lower substratum temperature (one reading was 17½° C. as against 18° C. for another substrate still less exposed than that under the *welleri* logs). In 1958, a third specimen was up the slope a bit and coiled on moist leaf duff under a small log or stick (a juvenile *P. yonahlosse* was found in a similar situation a few yards away, but adult *P. glutinosus* and *yonahlosse* were taken under larger shelters where the soil was more moist), and the fourth specimen was under bits of wood and leaf trash in a wet pocket by the stream on the flat nearby. A fifth specimen was taken elsewhere below the slope under a bit of wood near a rotten stump. Data on substrate temperature, immediate relative humidity, and substrate organic matter and free moisture were gathered for these three specimens (Table I) in order to describe the *welleri* environment further. Near values for the subshelter relative humidities were obtained by partly raising the shelters and immediately spinning a Bacharac sling psychrometer in the shelter space. The spin radius is only 6.5 inches, and the plastic-protected thermometer bulbs can safely brush the substratum. Substratum samples were packed into plastic vials, tightly sealed, and later duplicate subsamples were weighed before and after oven drying and ashing, and the average values used. Similar data were taken for comparison (Table I) from three *P. yonahlossee* taken up on the slope. The first was on mixed deciduous and hemlock duff under a rock, the second under a thick mat of moss (commonly called fern moss) covering a log, and the third in a mass of wet red rotten wood under a log.

The 12 *welleri* from Grandfather Mountain were taken on substrata of 8° C. Nine were under rocks at the surface of the talus,

TABLE I.—Limestone Cove Substratum Data.[1]

SPECIES OF PLETHODON	Substratum type	Substratum temperature	Percent ash (mineral matter)	Percent combustible matter (an organic index)	Percent free water	Ratio of free water to dry weight	Percent immediate relative humidity
3rd *P. welleri*[2]	leaf duff	20°C	67½	10½	22	.280	87
4th *P. welleri*	humus	20°C	62	15	23	.295	95
5th *P. welleri*	dark humus	20°C	60½	15	24½	.330	89
1st *P. yonahlossee*	mixed duff	19°C	72	9	19	.230	95
2nd *P. yonahlossee*	humus	21°C	65	10	25	.335	89
3rd *P. yonahlossee*	rotten wood	20°C	63½	9½	27	.375	87

1. See text for methods.
2. See text.

one was under a flake of rock in a cliff crevice, and two were under one large piece of bark (*P. w. welleri* have also been found inside rotten logs, according to the data accompanying Chicago Natural History Museum (CNHM) specimens 45921-38). The substrata they rested on were rock, moist black dirt, dirt and duff, and dry conifer needles in one case. This last animal was found facing out under the edge of a flat rock just before the fog and rain began (the relative humidity under the shelter site was 93% as against 81% at chest height). The animal lay in a slight trench or "runway" in the conifer duff, which led down to a small damp area under the lower side of the rock.

On Grandfather Mountain all of the animals were found in, on, or next to a coarse talus of non-igneous rock (the spaces between the rocks descended at least several feet), and the slope by which the animals of Limestone Cove were found was also partly of this composition. The association with this talus agrees with hypotheses presented earlier (Thurow, 1956a: 353). Although nocturnal surface activity which I observed in such forms as *P. cinereus, glutinosus,* and *metcalfi* may only involve emergence from under surface cover, greater vertical diel migrations are possible in animals like *P. welleri* and *P. dorsalis* which have some association with a rocky substratum.

Such movements of forest floor animals have been compared with the vertical movements of aquatic plankton, and may involve escape movements, weather responses, diel, and seasonal cycles.

There are observations confirming deeper movements in *P. dorsalis*. In Indiana, I have followed a group down through about a foot of talus to solid rock, and observed them futilely trying to burrow deeper. They were also found along the seepage passing under small talus piles that were dismantled, and at the top of larger piles where the surface run-off entered and at the bottom where it emerged—suggesting penetration to depths of tens of feet. I have found them in a cave over eight feet below the surface, and Hahn (1908) found them 25 feet below the surface. Mohr (1952) and a communication from Mr. W. T. Austin indicate that they may go still deeper, seasonally. Although there has been no observation of such deep retreat in *welleri*, there are suggestions that it has similarities of habits and habitat, one being its usual rarity at the surface. In a similar talus habitat on the lower mountain slopes near Gatlinburg, Tennessee, *P. dorsalis* shows the same scarcity.

The above remarks are not meant to imply a fundamental difference between *P. welleri* and *P. dorsalis* versus such species as *P. cinereus* and *P. glutinosus*, as it is more or less generally known that all species of *Plethodon* tend to retire below the surface when conditions are unfavorable and Taub (1961) shows that this is true for *P. cinereus* at other times also. However, there does appear to be a difference in ability to exist on a variety of substrata. *P. glutinosus* and *cinereus* are found on alluvium or glacial till miles away from any area underlain by rock, whereas *welleri* and *dorsalis* characteristically are not. Although such "preferences" or associations are not absolute, they become clearly evident when colonies of two species are compared in one area for several years, so that variations in surface activity and dispersal due to season and weather are put in proper perspective. *P. cinereus* and *dorsalis* were observed this way near Bloomington, Indiana, and did show such association with different substrata, although they could be found in close proximity, and even under the same log in border areas (Thurow, 1955). These impressions were supported by observations made over most of the ranges of these two species in the United States.

On the forest floor at Limestone Cove the salamander associates of *P. welleri* were one salamandrid, *Diemictylus v. viridescens*, and the plethodontids *P. glutinosus, P. yonahlossee*, and to a lesser extent *Desmognathus monticola* and *D. ochrophaeus carolinensis*. *Plethodon welleri* was more or less at the foot of the slope, *yonah-*

lossee was up on the slope, *glutinosus* was all over though perhaps less abundant on the slope, the one preadult *Diemictylus* was down on the flat under a log, and the two species of *Desmognathus* tended to be near the streamlet bank here, and were most abundant under trash in the moist sandy streamlet bed. All of these species were taken less than 50 feet from *welleri*, and some much closer. *D. quadramaculatus* was taken from a rocky tributary to the streamlet, less than 100 yards from *P. welleri*. Slightly more *P. yonahlossee* were seen on the surface than *welleri*, and *glutinosus* were over twice as abundant.

The only salamander associate on Grandfather Mountain was one *P. metcalfi*, in close proximity, under a log. Previous records of *welleri* salamander associates are for *P. metcalfi* (Walker, 1931, 1934, and Snyder, 1946), *P. cinereus* (Walker, 1934), and *D. ochrophaeus carolinensis* (Walker, 1931, and the data with CNHM 93022-6). Bogert (1952) recorded *P. welleri, P. metcalfi, D. o. carolinensis, D. wrighti*, and *Eurycea bislineata wilderae* between 5,200 and 5,720 feet on Mt. Rogers, but does not describe the intimacy of association.

FOOD HABITS

The digestive tracts of GRT 1639-50 were examined, although they had not been preserved immediately, and the items which were identified are listed in Table II. The animals had been kept in a glass jar with a little moss at 10° C. for almost three days and then anesthetized, six being preserved then and six less than 24 hours later. Although the remains found in the digestive tracts were only part of the food originally eaten, it is better than no data at all, and cannot be said to contain false items of diet. Any items that had been obtained from the moss during captivity were still food obtained from the natural habitat, as this was the same moss upon which and in which the salamanders were collected. Enough data has been accumulated on the food habits of *Plethodon* (*e. g.*, Bishop, 1941, and Pope, 1950) to indicate that they eat at the surface of the forest floor as well as other places, and take what they can get of what is available. Although I have not observed *P. welleri* feeding, I have observed *P. cinereus, dorsalis*, and *glutinosus* feed this way in terraria for periods of months and years, and the anatomy and observed habits of *welleri* are such as to make it doubtful that its general feeding habits are any different. Actually, the remains from the digestive tracts represented animals of such size and numbers that it was impossible for all of them to have remained hidden in the piece of moss when it was placed in the jar (this moss was

TABLE II.—Food Items of *Plethodon w. welleri*.

Collection number (GRT 1639–50)	1639	–41	–40	–42	–43	–44	–50	–49	–45	–46	–48	–47	Totals
Head width in mm.	5.9	5.6	5.4	5.1	4.9	3.6	5.5	5.5	5.2	4.9	4.8	4.7	
Food items													
Arthropoda													
Unidentified fragments	X	X	X	X	X	X	X	.....	X	.....	X	X	10X
Arachnida													
Chelonethida (pseudo-scorpions, 1 sp.)	2	1	2	3	.....	.....	3	1	1	.....	.....	1	14
Araneida (spiders, gray or brown ground types)	.....	.....	2	1	.....	1	.....	.....	.....	.....	.....	.....	4
Acarina (mites)													
1 red-brown sp.	.....	.....	.....	2	.....	4	3	.....	.....	.....	.....	5	14
Other sp.	1	.....	.....	1	.....	.....	2	.....	1	.....	.....	3	8
Insecta													
Unidentified parts	X	.....	.....	X	.....	.....	X	.....	.....	.....	.....	.....	3X
Unidentified eggs	.....	.....	.....	.....	.....	.....	10	.....	.....	.....	.....	.....	10
Collembola?	X	X	.....	X	.....	.....	.....	.....	.....	.....	.....	.....	3X
Hemiptera	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1
Lepidoptera													
1 sp. of larva	.....	.....	30	12	.....	.....	11	.....	.....	.....	.....	.....	53
Wing scales?	X	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1X
Diptera (one wing, of *Helomyzidae*?)	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
Coleoptera													
Unidentified parts	X	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1X
Adephaga													
Carabidae (ground beetles, 1 sp.)	5	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	5
Polyphaga													
Unidentified	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
Staphylinidae (rove beetles, 1? sp.)	3	.....	.....	1	.....	.....	.....	.....	1	.....	.....	.....	5
Wood or bark	.....	X	.....	.....	.....	.....	.....	.....	X	.....	.....	.....	2X
Stones	.....	.....	.....	.....	.....	.....	.....	X	.....	.....	.....	.....	1X
Miscellaneous debris	.....	.....	.....	.....	X	X	.....	X	.....	.....	X	.....	4X
Total individuals	12	1	34	20	.....	5	29	1	3	.....	.....	11	116

rinsed and squeezed out in water an hour or so later), and the state of digestion of almost all of these remains precludes their ingestion one or two days before death. All of the digestive tracts were partly empty, and contained only the less digestible remains. One of the six which were kept alive the longest (GRT 1645-50) had an empty digestive tract, and three others had empty stomachs. Five of the six killed before three days had remains in the stomach as well as the small intestine and colon. Incomplete chitinous exoskeletons, and parts of the same individual food item found in the rectum and the stomach of one salamander, indicate that all parts of a meal do not proceed through the digestive tract with equal speed.

The size of the food items was estimated with an ocular micrometer. The largest beetles were about 1.5 x 3.6 mm., the hemipteran 1.8 x 4.7 mm., the caterpillars .2 or .3 x 3.6 mm., the mites no more than .73 x 1.1 mm. for the most common species (one was wider, another smaller), and the usual position of the pseudoscorpion claws is such that they increased the total width and length to as much as 4.7 x 4.7 mm., although this can be reduced and the width of the carapace was only 1.0 mm. or less. All these animals were eaten by salamanders with a maximum head width (taken near the angle of the jaws) of 4.7 to 5.9 mm. (Table II). The juvenile, which contained mites and a slightly larger but compressible spider had a head width of 3.6 mm. Comparison of these data with those presented by Pope (1950: 90-93) for *P. yonahlossee* and *P. glutinosus* shows that considerably smaller food objects are taken by *welleri*. Although this is a small and incomplete sampling, additional data will probably confirm that certain larger and more active food items of the other two species are indeed missing or unimportant in the *welleri* diet. Field observations indicate that this species with its relatively smaller and shorter legs is less active and agile than the eastern Large Plethodons (defined by Grobman, 1944: 266), although it can jump in the manner described for *P. cinereus* (Dunn, 1926: 169—the juvenile jumped downward about six inches from my hand into a quart jar, landing on the vertical wall). So most of the commonly encountered snails, earthworms, and centipedes, for instance, would seem to be either too large or too active for *welleri* to ingest. Additional data will also reveal whether the greater importance of Arachnida in the *welleri* diet as compared to other small *Plethodon* such as *cinereus* (Bishop, 1941) is characteristic.

The ecological stratum indicated by the *welleri* food items is definitely the subforest floor. All of the food items could have been

taken under surface cover. Few, if any, of the forms are characteristically found out on the forest floor, except at night, and the mites, pseudoscorpions, staphylinid beetles, and possible collembolans, in particular, are known to occur below ground as well as just below surface cover.

One *welleri* contained a small piece of bark, another a stick .5 x .5 x 4.0 mm., and another two stones, the larger measuring 1.3 x 1.8 x 2.0 mm. Apparently large items can be ingested accidentally with prey.

P. welleri can eat its own shed skin under certain conditions at least, as one was found in the stomach of one of the specimens from Limestone Cove kept over two weeks without food at 18° C. (this was also found for *cinereus* in nature, by Blanchard, in Bishop, 1941).

REPRODUCTION, GROWTH, AND MATURATION

The data here consist mainly of body length measurements, dissections of the above-mentioned live specimens (GRT 937-8, 1548-9, and 1639-50), and the American Museum of Natural History (AMNH) series 5448 (11 specimens), collected from Mt. Rogers on July 8, 1949, plus observations of secondary sex characters in the above specimens and those listed earlier (Thurow, 1956a). Body length was measured from the snout to a point midway between the posterior margins of the hind limbs with a dial calipers. The measurements referred to in the following discussion (and in fig. 1) were all taken from preserved specimens. The relationship between this measurement, the same in life, and the preserved length from snout to anterior margin of the vent, is indicated by listing them in that order for GRT 1548-9 and 1639-50, after arranging these by size: 22.6-23.5-23.5, 31.1-32.0-32.9; 19.4-20.0-20.0, 29.7-30.4-30.7, 30.4-31.2-31.2, 30.9-32.0-32.4, 32.9-34.3-34.4, 32.9-33.7-34.7, 33.5-34.2-35.1, 34.2-(-)-36.2, 36.4-38.4-38.4, 37.0-38.0-39.4, 37.4-(-)-39.4, and 38.3-39.8-40.6. These measurements and many others of small *Plethodon* indicate that for the range of 20-40 mm. the most accurate conversion from well preserved to live body length (as defined here) in round numbers, is made by adding 1 mm. Smaller animals shrink less and larger ones shrink more.

Males collected in September (GRT 937-8) and in April (adults of 1639-50) had sperm in their swollen vasa deferentia, which indicates both spring and fall breeding activity. Males collected in the summer (AMNH 54448) did not have swollen vasa deferentia, and this and the summer regression of secondary sex characters implies that they do not mate then. Organ (1960) observed recently cap-

tured *welleri* from the Mt. Rogers-Whitetop Mountain area in the months of April-June and August-October, and witnessed courtship and male combat in October only. One of my males from Grandfather Mountain (GRT 1645) has a bite mark on the base of its tail which is probably due to the same kind of male combat. All this gives evidence that *P. welleri* breeds in April and possibly early May, but that it does not usually breed again until October. There are no data for the intervening winter months.

The development of secondary sex characters did not vary noticeably over the range of *P. welleri*, although such geographic variation has been reported in *Plethodon* (Hairston and Pope, 1948, Thurow, 1956b). This is not surprising in that there are no great geographic differences within the small range of the species, and very few differences have been demonstrated in other characters (Thurow, 1956a).

Seasonal variation of secondary sex characters does occur in *P. welleri*. Adult males collected on April 30th (from GRT 1639-50) had definite raised slightly oval mental gland pads of the type described for *P. dorsalis* (Thurow, 1956b) but slightly smaller. Although the relative development of these pads was stronger than in material seen previously, the size and the color contrast and thickness are still definitely less than in *P. glutinosus*, several of the *P. jordani* group, *P. cinereus*, and even *P. dorsalis*. *Plethodon welleri* summer material examined earlier usually had no visible mental gland or only a vague thickened and lighter colored area. Organ (1960) observed well-developed mental glands in the fall (mainly in October), but not in the summer or spring. He may have obtained negative data in the spring for the same reason I obtained largely negative data in the fall (Thurow, 1956a:348)—through a paucity of males of sufficient size (see below) that were far enough from summer.

The ventral hedonic glands are not well developed in male *welleri* (Thurow, 1956a) and are less extensively distributed than in large eastern *Plethodon*. Rarely (as in the *P. w. welleri* type specimen, USNM 84135) they not only occur on the ventrum of the tail and around the vent, but on the posterior belly, pectoral, gular, and cheek areas. Hedonics occur just above the cheek (Thurow, 1956a:348) less rarely (*e. g.*, in three of the eight AMNH 54448 males) and these might be useful when the courting male circles underneath the chin of the female (Organ, 1960:293). There is little seasonal variation in the appearance of the glands other than a possible distension due to a greater quantity of secretion, and this

was not observed. Although in breeding condition, the adult males of GRT 1639-50 did not show noticeably larger glands in April than some similar size males did in the summer, and the characteristic orange secretion was not present. This orange secretion was present in at least one of the two males collected in Limestone Cove in September (GRT 937-8), which suggests the interesting possibility that the activity of these glands may be greater in the fall than the spring, and may not parallel the activity of the mental glands.

The vent and nasolabial areas of the male may be expected to be more swollen during breeding seasons. This was observed in the April specimens. Weakly developed nasolabial "tubercles" were noted in the two males collected in September (GRT 937-8), and Organ (1960) noted that a courting October male had a swollen vent.

The general conclusion is that male secondary sexual characters tend to be better developed or more active in the spring (especially in April), that they regress in the summer, and that they show better development again in the fall (especially in October). If *P. welleri* is like *P. dorsalis* it should show some mating activity and development of secondary sex characters in periods of mild weather during the winter (Thurow, 1955:52-3). Without specimens, it is not known whether the characters regress somewhat in the winter, but, judging from other species, such regression is probably less marked than in the summer. It is also possible, but not proved, that the seasonal rhythms in breeding activity and development of secondary sex characters may be shifted slightly at the extremes of the over 3,000 foot altitude range.

The development of male secondary sex characters clearly varies with body length (and this means with age) as well as seasonally. When GRT 1639-50 and the other series are each ordered by size it can be seen that the development of the mental gland, the ventral hedonic glands, the size of the two flat lobes at the posterior margin of the vent, and the swelling of the vent and nasolabial areas all increase with body length. The unpigmented vent of immature animals becomes increasingly invaded by melanophores in the adult, the invasion proceeding from the middle on each side.

Sexual dimorphism of the teeth is lacking or poorly developed in *P. welleri*, so no age or seasonal differences were observed. No specimen showed enlargement of any of the premaxillary teeth, and the marginal tooth row does not stray outside the fleshy "lip" or jaw margin ridge in the area between the nasolabial grooves, as it does in some male *P. cinereus*.

The few females that were examined showed no externally visible seasonal changes. The usual lack of ventral hedonic glands agrees with the situation in other small eastern *Plethodon,* but not that for most large eastern *Plethodon.* The vent becomes invaded by pigment with age, as in the male, and transverse folds, or pleats, develop in the margins.

No females had ova ready for deposition. Oviposition typically follows the mating season in *Plethodon,* and the *P. welleri* male data indicate that this ends in the spring. Thus, oviposition would be expected to take place in the summer, as it does in other small eastern *Plethodon* such as *cinereus* (Bishop, 1943), *dorsalis* (Mohr, 1952, Thurow, 1955), *nettingi* (Brooks, 1948), and *richmondi* (Duellman, 1954, Wallace and Barbour, 1957). This has been established for *welleri* by Organ (1960), who found egg clutches from mid-August to early September; he describes the eggs, egg sites and attendant female behavior, the embryos, and the resulting hatchlings. His description of the nest site (beneath a thick layer of moss on rotten conifer logs) does not suggest a deep substratum retreat for oviposition. These nests were at 5,200 feet or higher, however, and at lower altitudes the nests may be deeper. It appears likely that *welleri* eggs could also be deposited below the surface in moist rock crevices, since such nesting sites have been described for *cinereus* (Cochran, 1911:341-6), *dorsalis* (Mohr, 1952), and *richmondi* (Wallace and Barbour, 1957). The retirement of some females to nest sites could help explain the unequal sex ratios in the GRT 1639-50 series of April 30th (six mature males and apparently one female) and the AMNH 54448 series of July 8th (eight males among 11 adults). Such unequal ratios have been correlated with oviposition season in a much larger sampling of *cinereus* (Test and Bingham, 1948:371).

Since hatchling *P. welleri* are similar in size and are apparently born in only one season of the year (Organ, 1960), as in other *Plethodon,* age groups should be distinguishable in size-frequency curves before a slowed growth rate and cumulative differences in individual rates cause these groups to merge—as in other *Plethodon* (*e. g.,* see Highton, 1956, fig. 6). The upper row of figure 1 is a frequency distribution of some body lengths from CNHM 45921-38, collected August 10, 1946, on Grandfather Mountain; the lower row is a similar arrangement of these measurements from GRT 1639-50. The curved arch represents the hatchling length (Organ, 1960—the effects of preservation and the different measurement of body length would cause no more than 1 mm. difference in animals of this

FIGURE 1.—Size-frequency graphs of Grandfather Mountain *Plethodon w. welleri* for August 10, 1946, and April 30, 1960.

size). Although comparison of samples from different years may be questioned, it is known that *Plethodon* lives in a buffered environment which does not change greatly; I know of no evidence to suggest that either the climate or the habitat of *P. welleri* were greatly different on Grandfather Mountain in 1946 and 1960. And the fact that age groups for different years can be made out in *Plethodon* proves that conditions in those years do not cause such variable growth as to cause the younger age groups to disappear. Judging from observed growth rates of the similarly-sized *P. dorsalis* in terraria (Thurow, 1955, fig. 2) the 19 and 21-3 mm. *welleri* lengths in figure 1 (rounded off to mm.) represent growth through the first year (the 22.6 mm. specimen from Limestone Cove in July also appears to be a yearling). Similarly, the gap between 19 and 30 mm. in April represents not one but two years, the missing age group being represented by the 27 mm. length in the upper row. The same year group is almost certainly represented by body lengths of 26.5, 25.4, 24.8, and 26.4 from the same locality, from collections on August 8, 1937 (CNHM 93012), April 19, 1938 (CNHM 92997, 93000—these two in the group born one year after CNHM 93012), and August 27, 1930 (USNM 84137). The 30-31 mm. lengths in the bottom row of figure 1 probably represent specimens in their third year, but the 30 mm. length of the upper row might belong to an animal in its second year, and measurements of other animals make it clear that age groups are not clearly separable above 30 mm.

Examination of museum material makes it clear that males mature between 25-35 mm., and this can be determined more narrowly. The six males larger than 32 mm. in April (fig. 1, second row) had pigmented vasa deferentia swollen with sperm and were mature, but the two 30 mm. males were immature in that the small vasa deferentia held no sperm and were almost unpigmented, although the testes showed some enlargement and some pigmentation. A similar situation exists in a 31.1 mm. specimen taken from Limestone Cove in July and killed August 15. The males of 31 and 30½ mm. collected from Limestone Cove on September 16 (and killed on the 24th) had vasa deferentia swollen with sperm and were mature, although the secondary sex characters were weakly developed. A male collected August 27, 1930, from Grandfather Mountain (USNM 84136), also showed some weak development of the secondary characters, but was not dissected. The eight males collected from Mt. Rogers on July 8th (AMNH 54448) were 36-41 mm. and clearly mature in that the vasa deferentia were darkly pigmented though shrunken, and secondary sex characters were present though weakly

developed. All this strongly suggests that most male *P. welleri* all over the species range mature in the fall at about 30 mm. body length (this corresponds to about 31 mm. in live specimens, and 32 mm. in live specimens measured from snout to anterior vent angle), and that spermatogenesis takes place the preceding summer.

The age of male maturity is less certain. All males should reach breeding condition by three years, in the fall, but some large males may also reach breeding condition at two years.

The maturation size and age of female *welleri* are more difficult to determine. Spring females with enlarging eggs are clearly mature, but if these same animals court in the preceding fall before the eggs enlarge they could also be called mature at that time, and these body lengths could be obtained only by measuring specimens that were observed to court or contained spermatophores. Highton (1956) demonstrates that oviposition size may be quite variable in *Plethodon*. Organ (1960) gave the snout-to-posterior-vent-angle measurement of 42.5 mm. for his smallest brooding female. This was probably taken in life, and would be roughly comparable to a length of 38 mm. as measured here. The 22.6 mm. female collected from Limestone Cove in July, and the females of 30.9 and 33.5 mm. in figure 1 are clearly immature, with about 20 or more uniformly small eggs, none over .6 mm. in diameter. The 37.4 female (fig. 1) had some enlarging ova as large as 1 mm. in diameter. These probably would have reached ovipositing size by the summer (about 3.5 mm. in related species, and consistent with the 5.5-6 mm. of Organ (1960), as he measured the ova plus membranes). These scanty data and the data from males permit only the preliminary estimate that most females with enlarging eggs in the spring are over three years old and exceed 35 mm. in body length.

While the relative growth of some of the external dimensions of *P. welleri* has been illustrated (Thurow, 1956a), the relative growth of the viscera has received almost no study in *Plethodontidae*. Dissection of *P. welleri* (and other *Plethodon*) show that the length and bulk of the liver increase more rapidly than the length of the trunk, at least from hatching to maturity.

SUMMARY AND CONCLUSIONS

1. Photographs and a description of living *Plethodon welleri ventromaculatus* support its subspecific separation, as do examinations of additional museum material, but no additional fundamental differences are revealed.

2. Indications of a cryptic dorsal band in some preserved material appear to be absent in life, and no special juvenile pigmentation was noted in the smallest specimen.
3. A new locality for *P. w. ventromaculatus* is in Unicoi Co., Tennessee, in a limestone cove valley at 2300-2400 feet, at the foot of the northwest slope of Unaka Mountain.
4. There the forest is mostly hemlock, yellow birch, and *Rhododendron maximum*, rather than spruce-fir, and a locality on Grandfather Mountain also has hemlock and yellow birch.
5. The *P. welleri* from Limestone Cove were under small logs, and wood and leaf trash, and resting on duff or humus. The specimens from Grandfather Mountain were mostly under rocks of a talus pile, resting on rock, moist black dirt, dirt and duff, and once on dry needles. They also occur under bark, or in and under logs.
6. Summer and fall substratum temperatures at Limestone Cove were 20 and 18° C., all being lower than the air temperatures at chest height. Spring substratum temperatures of 8° C. at Grandfather Mountain were warmer than the chest high temperature of 6° C. A winter visit to the same site in freezing temperatures revealed no salamanders.
7. Although three near-shelter relative humidity readings for *P. welleri* and *P. yonahlossee* at Limestone Cove were the same (87-89-95% vs. 87-89-95%) and the amounts of free water in the substrata were similar (22-24½-23% vs. 27-25-19%), qualitative observations indicate that *P. welleri* can occur under smaller shelters and slightly dryer conditions than adult *P. yonahlossee* and *P. glutinosus* at Limestone Cove.
8. *P. welleri* at both localities were in, on, or near coarse non-igneous rock talus which permits deeper descent below the surface than does the substrata of some other *Plethodon* species. Such a deeper descent is described for *P. dorsalis* and suggested for *P. welleri.*
9. Previously unreported salamander associates for *P. welleri* are *P. glutinosus, P. yonahlossee, Desmognathus monticola, D. quadramaculatus* (found further from *P. welleri* and clearly with less habitat overlap), and *Diemictylus v. viridescens.*
10. Partly digested food identified from nine *P. w. welleri* included pseudoscorpions, mites, spiders, beetles, lepidopteran larvae and perhaps wing scales, one hemipteran, one fly, and possibly some collembolans. The size and nature of this food and of *P. welleri* suggests that its prey is smaller and maybe less active

than that of larger *Plethodon*. A higher percentage of arachnids and a more subterranean diet appear to be indicated than by the food items of *P. cinereus*.

11. Duplicate body length measurements give the general relationship between the snout-to-posterior-hindlimb-margin preserved length used here and live or snout-to-vent lengths.
12. Males had vasa deferentia swollen with sperm in April and September but not in summer, indicating spring and fall breeding activity.
13. No secondary sex character was observed to vary geographically, but male *P. welleri* secondary sex characters (mental gland clusters, ventral hedonic glands, which are further described, vent lobes, and nasolabial and vent swelling) do vary seasonally, showing greater development in the spring and fall, and regressing in the summer. The ventral hedonic glands varied only in that the orange secretion (which is not visible after preservation) was present in one or both males collected in September, but not in the males taken in April. The above male secondary sex characters become better developed with greater age and size, and the unpigmented immature vent becomes increasingly pigmented in the adult.
14. No seasonal changes were observed in females, but the margins of the adult vent also become pigmented, and become pleated or folded.
15. First year and second year age groups are distinguished in size-frequency distributions, and supported by observed terrarium growth rates in *P. dorsalis*.
16. Male *P. welleri* seem to mature at about 30 mm. (31 in life), and in the fall at three years of age, although some may mature a year earlier. Female maturation is more difficult to determine, but available data suggest that most *P. welleri* with enlarging ova in the spring are over three years old and exceed 35 mm. in body length.
17. The relative growth of the liver exceeds that of the trunk in immature animals of both sexes.

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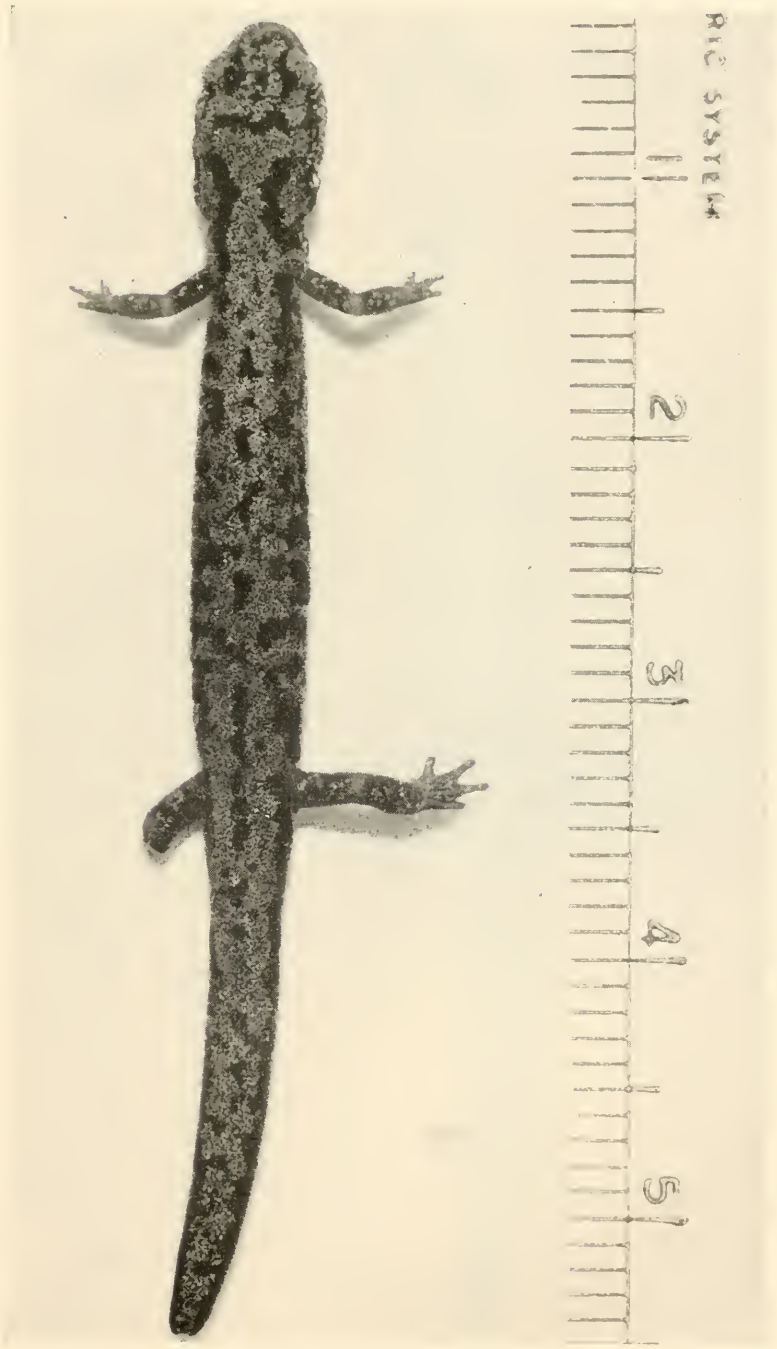

PLATE I.—*Plethodon welleri ventromaculatus,* dorsal view.

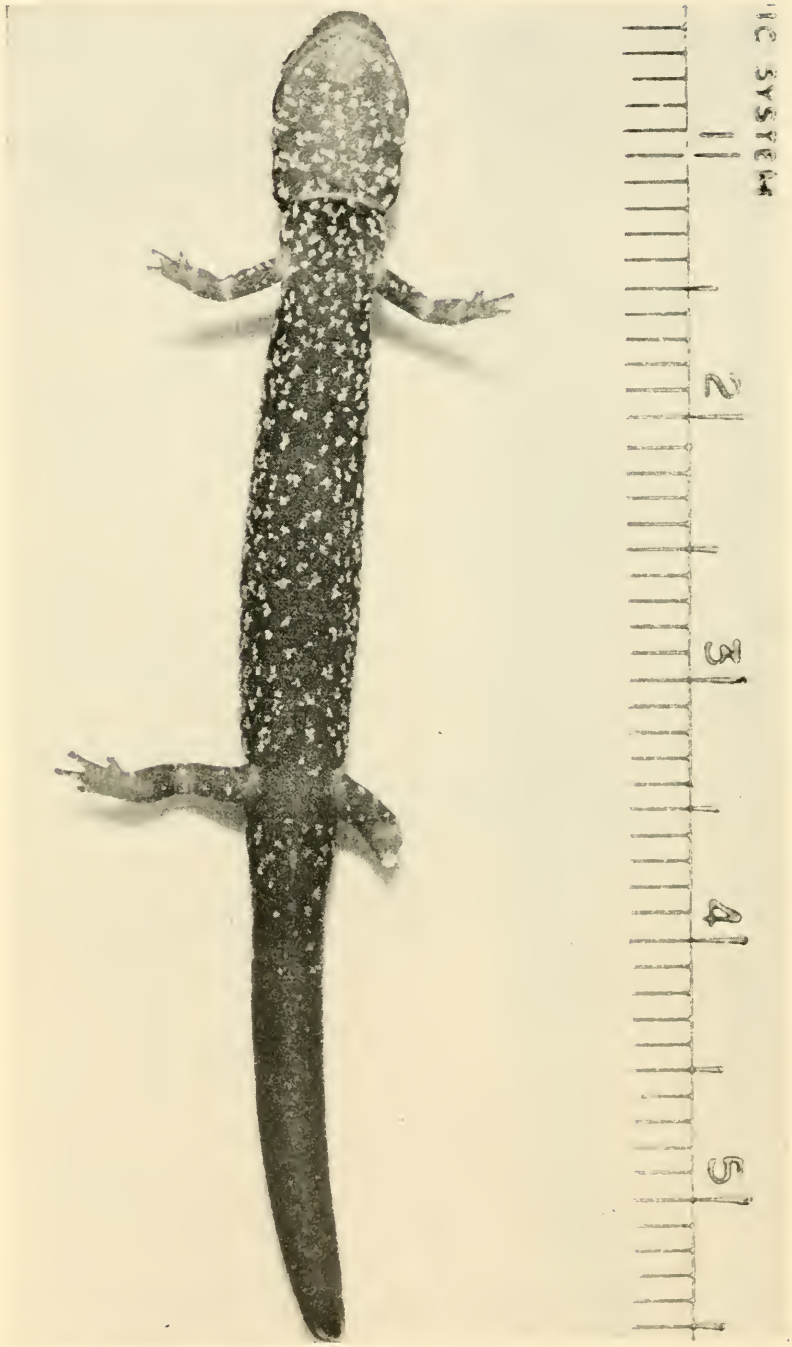

PLATE II.—*Plethodon welleri ventromaculatus,* ventral view.

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Indian Discomycetes

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ABSTRACT: The present study includes 185 known Discomycetes from India and 79 of these fungi are reported for the first time. Material of all these fungi (belonging to 62 different genera) except 44 species listed in Part II was examined in fresh or dried condition. Part III of this paper contains a descriptive key to the operculate Discomycetes whose material was examined in fresh condition. The species encountered in the literature and known to be misidentifications are reported separately. A complete bibliography of the Indian Discomycetes is given at the end of this paper. The key to the operculate species is based on morphological, anatomical and histochemical characteristics. The following species are included in this key: *ALEURIA aurantia* (Pers. *ex* Fr.) Fuckel, *A. rubra* Batra, *A. rutilans* (Fr.) Gillet, *ANTHRACOBIA melaloma* (Alb. & Schw. *ex* Fr.) Boud., *ASCOBOLUS carbonarius* Karst., *A. immersus* Pers. *ex* Fr., *A. magnificus* Dodge, *A. stercorarius* (Bull. *ex* Fr.) Schröt., *A. taxonomic sp. V.* Batra, *ASCOPHANUS holmskjoldii* E. C. Hansen, *A. glaucellus* Rehm, *A. ochraceous* (Crouan) Boud., *A. striatus* Thind, Cash & Singh (*A. taxonomic sp. XIII* Batra, 1960), *A. taxonomic sp. XII,* and *XIV* Batra, *CHEILYMENIA coprinaria* (Cooke) Boud., *C. pulcherrima* (Crouan) Boud., *C. theleboloides* (Alb. & Schw. *ex* Fr.) Boud., *COOKEINA sulcipes* (Berk.)

1. This is an incomplete presentation of the Indian Discomycete flora and an attempt to create a starting point for taxonomic studies of this group following modern concepts and using newer techniques. The term "Discomycete" is here used to include the orders Pezizales (with operculate asci) and Helotiales (with inoperculate asci). The larger part of the material covered in the checklist and the keys is based on our own collections made over a span of ten years beginning in 1951 while the senior author was a graduate student in the Department of Botany, Panjab University, India. From 1955 to date the work on Indian Discomycete flora was continued at Cornell University and at Swarthmore College.

In presenting this material the writers have intentionally refrained from full text descriptions of the genera and species. This is being done in a separate monograph which will be published in due course of time.

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Kuntze, *C. venezuelae* (Berk. & Curt.) Le Gal, *HELVELLA acetabulum* (L. *ex* Fr.) Quél., *H. crispa* Scop. *ex* Fr., *H. elastica* Bull. *ex* Fr., *H. ephippium* Lév., *H. calyciformis* Batt. *ex* Quél., (= *Acetabula sulcata* Pers. *ex* Fuckel), *H. lactea* Boud., *H. lacunosa* Afzelius *ex* Fr., *H. sulcata* Afzelius *ex* Fr., *HUMARIA hemispherica* Weber *ex* Fr., *HUMARINA lilacina* Seaver *sensu* Seaver, *H. semiimmersa* (Karst.) Seaver *sensu* Seaver, *LAMPROSPORA chopraiana* Batra, *L. planchonis* (Dun.) Seaver, *L. multiguttula* Batra, *L. spinulosa* Seaver, *L. taxonomic sp. VII* & *IX* Batra, *LASIOBOLUS equinus* (Müll.) Karst., *MORCHELLA angusticeps* Peck, *M. esculenta* L. *ex* Fr., *OCTOSPORA convexula* (Pers. *ex* Fr.) *comb. nov.* (*Basonym: Peziza convexula* Pers. *ex* Fr. Syst. Myc. p. 73, 1823.) *O. taxonomic sp. XVI* Batra, *PEZIZA badioconfusa* Korf, *P. brunneoatra* Desm., *P. gerardi* Cooke, *P. melaleuca* (Bres.) Seaver *sensu* Seaver, *P. pustulata* Pers. *ex* Fr., *P. repanda* Pers. *ex* Fr., *P. succosa* Berk., *P. vesiculosa* Bull. *ex* Fr., *P. taxonomic sp. XI* Batra, *PHILLIPSIA domingensis* Berk., *PITHYA cupressina* Fuckel, *PLICARIA papillosa* Batra, *P. pseudoplanchonis* Batra, *P. trachycarpa* (Curr.) Rehm *var. typica*, *PSEUDOPITHYELLA miniscula* (Boud. & Torrend) *Le Gal*, *PSEUDOPLECTANIA nigrella* (Pers. *ex* Fr.) Fuckel, *PTYCHOVERPA bohemica* (Krombh.) Boud., *PULVINULA discoidea* (P. Henn. & E. Nym.) *comb. nov.* (*Basonym: Barlaea discoidea* P. Henn. & E. Nym., Monsunia 1: 33.1900.), *P. mussooriensis* (Thind, Cash & Singh) *comb. nov.* (*Basonym: Lamprospora mussooriensis* Thind, Cash & Singh, Mycologia 51: 457), *PUSTULARIA bronea* (Peck) Kanouse, *P. catinus* (Holmskj. *ex* Fr.) Fuckel, *PYRONEMA omphaloides* (Bull. *ex* Fr.) Fuckel, *SACCOBOLUS kerverni* (Crouan) Boud., *OTIDEA leporina* (Batsch) Fuckel, *SCUTELLINIA cubensis* (Berk. & Curt.) Le Gal, *S. pygmea* (Clements) ? Le Gal (present authors' fungus = *Patella pygmea* (Clem.) Seaver *sensu* Seaver), *S. scutellata* (L. *ex* Fr.) Lambotte, *S. uliginosa* Batra, *SEPULTARIA arenicola* (Lév.) Massee, *S. arenosa* (Fuckel) Boud., *THECOTHEUS pelletieri* (Crouan) Boud., *TRICHARIA gilva* Boud., *TRICHOPHAEA albospadicea* (Grév.) Boud., *T. brunnea* (Alb. & Schw. *ex* Fr.) *comb. nov.* (*Basonym: Peziza brunnea* Alb. & Schw. *ex* Fr.), *T. gregaria* (Rehm) Boud., *T. himalyaensis* Batra (= *Sphaerospora tuberculata* Thind, Cash and Sethi), *WYNNEA americana* Thaxter, and *W. macrotis* (Berk.) Berk.

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ABBREVIATIONS AND GLOSSARY OF TERMS

The material examined is located in the herbaria indicated below. The names of these herbaria are abbreviated according to Lanjouw and Stafleu (1956).[4] Descriptive terms characterizing genera and species in the key to operculate Discomycetes are abbreviated and explained in the glossary.

The abbreviations "DU," "PUI," "Ahmad-," and "Butler-," which are the authors' coinage, are also explained below.

BPI	The National Fungus Collections, Crop Research Division, Plant Industry Station, U. S. D. A., Beltsville, Md.
CUP	Department of Plant Pathology, Cornell University, Ithaca, N. Y.
DD	Forest Research Institute and Colleges, Dehra Dun.
HCIO	Herbarium Crytogamiae Indiae Orientalis, Division of Mycology and Plant Pathology, IARI, New Delhi.
K	Herbarium, Royal Botanical Garden, Kew.
LAH	Panjab (Pakistan) University, Lahore.
LRB	Lekh Raj Batra (authors' personal herbarium).
DU	Mycological Herbarium, Delhi University, Delhi.
PUI	Herbarium Panjab (India) University, Chandigarh.
Ahmad	Personal Herbarium of Dr. Sultan Ahmad, Panjab (Pakistan) University, Lahore.
Butler	Herbarium of Sir E. J. Butler, former Imperial Mycologist, Government of India.

GLOSSARY OF TERMS

apiculate—a spore with one or two projections at one or both ends.

apothecium—(abbreviated as *apoth.*)—an ascocarp of Discomycetes in which the asci are arranged in a hymenium which is exposed from the beginning; a section of the apothecium parallel to the asci and paraphyses shows the following tissues: *hymenium, subhymenium,* and *excipulum* which is usually differentiated into two regions, the inner *medullary excipulum* and the outer *ectal excipulum.* (Figs. 1-3).

apothecial disc—(abbreviated as *apoth. disc*)—term used to describe the expanded part (bearing the hymenium) of a stipitate apothecium.

areolae—distinct areas of hymenium, bounded by sterile ridges, forming a honeycomb pattern.

cerebriform—brain-like, convoluted.

coprophilous—growing on dung.

4. Lanjouw, J., and F. A. Stafleu. 1956. Index Herbariorum. Part I. The Herbaria of the World. Ed. 3. Regnum Vegetabile 6: 1-224.

discoid—more or less flat; applied to an apothecium, in contrast to *concave* or *convex*.

ectal excipulum—(abbreviated as *ect. excipl.*)—the outermost tissue zone of the excipulum.

eguttulate—without a guttule.

excipulum—(abbreviated as *excipl.*)—the envelope of tissue or tissues covering the exterior of the apothecium (external to the subhymenium or hypothecium).

fasciculate—bundled together.

fimicolous—growing on dung.

flexuous—bent.

guttulate—having a drop of oil or fatty substance.

helvelloid—from the genus *Helvella;* applied to an apothecium of the following description: stalked, with a hollow or chambered stipe, fertile apex initially cupulate but with the marginal tissue continuing to grow so as to produce a saddle-shaped cap which may eventually become gyrose. (R. P. Korf, unpublished.)

humicolous—growing on humus.

hymenium—(abbreviated as *hym.*)—the fertile layer, in this case of the apothecium and composed of asci and paraphyses with occasional setae interspersed among them.

hypothecium—well differentiated layer of compact tissue lying immediately below the hymenium and giving rise to it; Seaver (1942) used the term *hypothecium* to designate the entire tissue lying between the hymenium and the "ectal layer" (= ectal excipulum).

lignicolous—growing on wood.

medullary excipulum—(abbreviated as *med. excipl.*)—the layer or layers of tissue lying between the ectal excipulum and the hypothecium.

morchelloid—from the genus *Morchella;* applied to an apothecium of the following description: stalked, with a hollow stipe, the cap becoming divided by sterile ridges into small fertile areolae.

operculatae—a group of Discomycetes in which the ascus dehisces by an operculum to discharge the ascospores.

operculum—a cover or lid, referring to the cap-like lid (usually circular) of an ascus.

paraphyses—(abbreviated as *para.*)—sterile hyphae interspersed among the asci.

pileus—the hymenium supporting part of a stipitate apothecium.

pustulate—having small, blister-like swellings.

scutellate—shield-shaped.

stipitate—stalked.

stroma—a mass of food storage tissue made up of vegetative hyphae (collectively known as medulla) which are surrounded by a well differentiated layer of cells or hyphae called the rind.

subiculum—a mycelial mat under a fruiting body.

terricolous—growing on ground or earth.

textura—(abbreviated as *text.*)—a web; a term applied by Starbäck (1895) [5] to hyphal tissue in discomycetes. The following classification of various textura by Starbäck and emended by Korf (1958) [6] is adapted from the latter author.

I. Short-celled tissue: the separate hyphae not distinguishable.
   A. Cells round to polyhedral, almost isodiametric.
      1. Cells rounding up, with intercellular spaces: *textura globulosa* (abbreviated as *text. glob.*).
      2. Cells polyhedral by mutual pressure, no intercellular spaces: *textura angularis* (abbreviated as *text. angul.*).
   B. Cells more or less rectangular in section, not isodiametric: *textura prismatica* (abbreviated as *text. prism.*).

II. Long-celled tissue: the separate hyphae easily distinguishable.
   A. Hyphae running in all directions, not parallel.
      1. Hyphae with their walls not united, usually with distinct interhyphal spaces: *textura intricata* (abbreviated as *text. intric.*).
      2. Hyphae with their walls united, without interhyphal spaces, usually forming a membranaceous tissue: *textura epidermoidea* (to be abbreviated as *text. epider.*).
   B. Hyphae running in one direction, more or less parallel.
      1. Hyphae with narrow lumina and strongly thickened walls, cohering: *textura oblita* (to be abbreviated as *text. obl.*).
      2. Hyphae with wide lumina and non-thickened walls, not cohering: *textura porrecta* (abbreviated as *text. porr.*).

tomentose—having a covering of short soft hair.

5. Starbäck, K. 1895. Discomyceten-studien. Bihang Kongl. Svenska Vet. Akad. Handl. 21, (Afd. III, No. 5):1-42.

6. Korf, R. P. 1958. Japanese Discomycetes. Notes I-VIII. Sci. Rept. Yokohama Nat. Univ. II. 7: 7-35.

INTRODUCTION

Butler and Bisby (1931) in their "The Fungi of India" (political India in 1931 included parts of Burma, Nepal and Pakistan) listed 69 fungi under "Discomycetes" out of which 46 are considered as Discomycetes by the author. All except one species, *Aleuria rutilans* (Fr.) Gill. = *Humaria rutilans* (Fr.) Sacc., were reported from what is commonly known as the Indian subcontinent. In recent years Ahmad (1949), Cash (1948), Sanwal (1953), Thind *et al.* (1957a to 1957d, 1959a, and 1959b) have contributed towards the Discomycete flora of India, bringing the total to 106 recorded species.

The present authors report 79 additional species, which are preceded by an asterisk. A complete bibliography pertaining to the Indian Discomycetes is also appended to facilitate future research. Genera and species of which the material was examined by the authors are arranged alphabetically under the respective families, and this constitutes Part I of the paper. Under Part II are enumerated the species reported in literature and where the material was not examined at this stage. The Part III includes a key to the operculate species, the material of which has been examined in fresh condition.

Distribution, time of collection and economic importance of Discomycetes

The Discomycetes are of world-wide distribution. We have collected both operculate and inoperculate species up to 16,000 ft. above sea level in the Himalayas where some humus or plant debris was available as substrate. They are more abundant in moist, temperate or subtropical areas than in tropical climates; and there are few reports about these fungi from the desert regions. Some of the species are exclusively parasites of a particular host and thus their distribution is indirectly limited with respect to altitude and other environmental conditions unfavorable for the host. While the most profitable time for collection of these fungi in Europe and North America is spring and autumn, late summer (July through September) appears to be the best season for the Discomycetes in the Himalayas and during the winter is best on the Indo-Gangetic Plains. Many species of the families Sclerotiniaceae and Pezizaceae (especially the genus *Ascobolus* of the latter), which appear to be early spring "bloomers" in the United States, form apothecia in winter in the Panjab plains, in early spring at the lower altitudes, and in late summer at the higher altitudes.

Except for the species of *Sclerotinia*, *Botryotinia* and *Monilinia* of the family Sclerotiniaceae, *Pseudopeziza* Fuckel and *Fabraea* Saccardo, of Helotiaceae, few Discomycetes appear to cause any appreciable damage to crop or ornamental plants. None of the Discomycetes reported in this paper are known to be poisonous or having caused a death. All known species of the genus *Morchella* are eagerly sought for as a delicacy for culinary purposes. Some species of *Helvella* were reported to be edible by many villagers in the Himalayas but the writers have not tried any one except *H. crispa* which apparently caused no upset stomach. *Gyromitra esculenta* Fries, which has so far not been collected from India but is known from Europe, North America and the Far East, will upset the digestive system of some people, and should be avoided.

General morphology of apothecium

The Discomycetes or cup-fungi form a distinct and natural subclass of Ascomycetes. The fruiting body or *ascoma* (also known as *ascocarp* or *ascophore*) in this case is called an *apothecium*. An apothecium is a disc-shaped receptacle covered on the upper surface by a palisade layer of unitunicate asci and paraphyses constituting the *hymenium*. The hymenium in an apothecium is exposed to the air in the young condition or at least on maturity. Ascospores in apothecia are usually forcibly ejected and known to be normally shortlived. A section running parallel to the asci in an apothecium indicates that the latter is composed of several morphologically distinguishable zones made of different tissues. The uppermost layer is the hymenium surrounded by an envelope of sterile tissue called *excipulum*. The compact tissue immediately below the hymenium and staining deeply is the *subhymenium* which is mostly composed of ascogenous hyphae and cells giving rise to paraphyses.

The excipulum itself may be differentiated into distinct zones. The outermost of these zones is called the *ectal excipulum*. The inner zone(s) of the excipulum in the tissue between the ectal excipulum and the subhymenium is known as *medullary excipulum*. The ascophore in the family Geoglossaceae is either terete or capitate. In the terete genera the hymenium forms a jacket around a columnar sterile tissue made up of hyphae running more or less parallel to each other. This tissue is known as medulla (fig. 3, 105, 123). The medulla may or may not be further differentiated into distinct zones. The subhymenium in most members of Geoglossaceae is sharply differentiated from the medulla. In the case of two mitrate or capitate genera of this family, *Verpatinia* Whetzel

and *Leotia* Persoon, the various tissue zones of the sterile portion of the disc are typical of an apothecium. The structure of these tissue zones is quite characteristic and is being used extensively for taxonomic work on Discomycetes. A key for recognizing such tissues is given in the glossary under the term "textura" which was originally used to describe a tissue by Starbäck.

The descriptive terms mentioned in the preceding two paragraphs in connection with apothecial anatomy have been used in many different ways and consequently create great confusion in Discomycete terminology. The term "hypothecium" was used to include the entire tissue below the hymenium, to refer to the subhymenium alone, or to include subhymenium and medullary excipulum, by different authors in the past. Similarly, the term "excipulum" was used to describe the ectal excipulum alone; and the medullary excipulum, as mentioned above, along with subhymenium, was referred to as hypothecium.

The shape, size, texture, and color of the apothecia is very variable. There are several modifications of the basic discoid shape and the apothecium may be pezizoid, helvelloid, morchelloid, verpoid or gyromitroid. They may be terete as in many Geoglossaceae or mitrate as in *Leotia* of the same family. The apothecia may be sessile, subsessile or distinctly stipitate. In case of stipitate apothecia, the stalk of the apothecium is referred to as *stipe* while the receptacle is called *pileus.*

Ectal excipulum

The ectal excipulum is quite characteristic for a species, a group of species in a genus, or even for an entire family. Thus the family Hyaloscyphaceae has an excipulum made up of cells which are rectangular in shape and usually thin walled yet in Dermateaceae the cells are globose to subglobose. The cells of ectal excipulum may be hypha-like and elongate as in case of the genus *Maublancomyces* Herter or may form a fasciculate tomentum as in the genus *Phillipsia* Berkeley, *Cookeina sulcipes* (Berkeley) Kuntze or many species of the genus *Helvella* L. *ex* Fr. In the last case, the cells of fasciculate tomentum are globose, subglobose, drum-shaped, or even rectangular and soon break apart on application of pressure (figs. 81, 82).

The cells or hyphae of the ectal excipulum may be modified as flexous, branched or unbranched hairs. Such hairs are of considerable taxonomic value. Thus the hairs in the genus *Sepultaria* (Cooke) Lambotte are thin walled, pale brown and flexous; in

Leucoscypha Boudier they are flexous and white; in *Sarcoscypha* (Fries) Boudier they are hyaline and form a felt; and in *Pseudoplectania* Fuckel they are black, and undulating or contorted. In many other cases the hairs may be stiff, erect and sharp pointed or acute, and quite distinct from the adjacent cells or hyphae. These hairs are usually thick walled and soon become septate. The hairs in the genera *Cheilymenia* Boudier, *Scutellinia* (Cooke) Lambotte and *Desmazierella* Libert are erect, rigid and pointed while in case of *Anthracobia* Boudier, *Melastiza* Boudier and *Jafnea* Korf, they are somewhat flexous, brown, and with blunt ends. The site of origin of the excipular hairs is also characteristic of some genera such as *Scutellinia* and *Cheilymenia* where they arise from the medullary excipulum and are usually forked or sometimes palmately branched near the base. The surface of the hairs may be smooth or verrucose as in the case of the genera *Dasyscyphus* S. F. Gray or *Cistella* Quélet.

In addition to the hairs on the outside of the apothecium, the genus *Trichoglossum* Boudier of Geoglossaceae, the genus *Desmazierella* of Pezizaceae, and many members of Hyaloscyphaceae, have some hairs in the hymenium or near the marginal paraphyses. Such hairs have sometimes been referred to as setae. The marginal tissue of the apothecium may also be characteristic and can be used to separate different species.

Medullary excipulum and subhymenium

Unlike ectal excipulum, these two tissues are less characteristic and of limited taxonomic value. In many cases there is no sharp distinction between the subhymenium and the medullary excipulum, which in itself is of some taxonomic value. The medullary excipulum may be of compactly placed isodiametric cells or more often of textura intricata or of textura porrecta. As mentioned above, some of the hyphae in the medullary excipulum may give rise to hairs which push their way through the ectal excipulum and form typical tomentum as in the genera *Scutellinia* and *Cheilymenia*. In a group of genera such as *Ombrophila* Fries, *Sphagnicola* Velenovsky and *Coryne* Tulasne, belonging to the family Helotiaceae, one encounters a medullary excipulum which is "floating" or embedded in a mucilaginous matrix. Another group of genera such as *Bulgaria* Fries and *Ascotremella* Seaver has both ectal and medullary excipulum in a matrix, while there are still other cases like the genus *Galliela* Korf where ectal excipulum alone is mucilaginous. The mucilaginous character of these tissues appears to be associated

with other important features of these genera which undoubtedly appear to be related to one another. It is our opinion that the genus *Leotia* Persoon, considered by many as a member of the Geoglossaceae, may be related to the genera of the Helotiaceae.

The hymenium and its constituents

The hymenium in most Discomycetes is even but may become uneven, wrinkled or grooved with maturity. The general appearance of asci, paraphyses and ascospores, their color and other characteristics play an important role in the taxonomy of Discomycetes. The characteristic color of the hymenium is imparted by various pigments residing in the paraphyses. The ascus wall or the ascospore wall seldom have any pigmentation. The pigments in the paraphyses may be located in small granules or diffused throughout the cell.

The asci

The asci in general are cylindrical and gradually tapering towards the base. They may be clavate as in many Helotiales or considerably elongate as in the genera *Sarcoscypha, Cookeina* Kuntze, *Phillipsia* and *Pseudopithyella* Seaver and abruptly narrowed into a short base. As a rule the asci are 8-spored but 16-, 32-, 64-, and 72-spored asci are observed in the single genus *Ryparobius* Boudier. The asci in *Thecotheus* Boudier, a monotypic genus, are uniformly 32-spored. Asci with spores fewer than eight are also known in many cases and *Ptychoverpa* Boudier has two large spores in each ascus. A large number of asci in the majority of Discomycetes mature at the same time and the ascospores are forcibly ejected as miniature clouds. The asci in Geoglossaceae and some members of the Helotiaceae discharge their spores one by one through the ascostome.

Operculate vs. inoperculate asci

Emile Boudier (1828-1920), a great French mycologist and undoubtedly the father of the modern Discomycete taxonomy, observed that there are two distinct methods by which the asci release ascospores in this group of fungi.

One group of Discomycetes releases its ascospores by the formation and subsequent removal of a lid or an operculum along a circumscissile line near the apex of the ascus. The operculum can be usually seen attached on one side near the tip of an ascus when freshly collected material is mounted in iodine solution. The second group of Discomycetes releases its ascospores through a simple

apical pore and without any lid or operculum. The ascospore exit in either case is known as ascostome which may appear irregularly fringed in many cases. The site of an operculum can be well demonstrated in comparatively younger asci of *Thecotheus pelletieri* (Crouan) Boudier by mounting fresh or dry material in iodine solution. The circumscissile line and future site of the operculum stains dark brown and a faintly delimited groove is perceptible. The presence of operculum or apical pore are not difficult to observe in fresh material although there may occasionally be some doubt as to the nature of dehiscence of asci obtained from dried material. This doubt may be soon eliminated by studying the other characters which are associated with the two types of ascus dehiscence. Boudier was so impressed by this basic distinction of operculum *vs.* pore for spore release at the ascus tip, that he designated the former as the *Operculate* and the latter as *Inoperculate* Discomycetes.

The ascospores of operculate Discomycetes are usually globose to ellipsoid with rounded or obtuse ends, always non-septate or unicellular, with their epispore frequently ornamented with callose-pectose markings. The ascus tip after the removal of the operculum appears to be truncated or obtuse. These forms are usually humicolous, terricolous, fimicolous, less often lignicolous, or parasitic. In contrast to the operculate series, the ascospores of inoperculate Discomycetes are usually ellipsoid to elongate, with acute or narrow ends, rarely globose, often more than one-celled and the epispore is not known to be ornamented. The ascus tip is greatly thickened and remains acute throughout. In many inoperculate Discomycetes, the ascostome is stuffed with an amyloid plug which sometimes stains intensely with iodine solution. The presence of this plug should leave no doubt as to the inoperculate nature of an ascus. The ultimate fate of this plug is not known but in some cases it is believed to be shot out by osmotic pressure built up inside the ascus. The apothecia of the inoperculate Discomycetes are predominantly lignicolous or parasitic and less often terri-, humi-, or fimicolous.

The Tuberales resemble the true Discomycetes in the formation of asci in a hymenium, presence of true paraphyses and by the presence of ornamentation on the epispore. They are predominantly subterranean and the asci do not release the spores by forcible ejection. A true ascostome is absent from the ascus tip and the ascus wall probably breaks away by irregular fissures, thus releasing the spores inside the ascocarp cavity.

The iodine reaction and the asci

Great significance is attached to the presence or absence of bluing reaction of the asci in Discomycete taxonomy and many authors have gone so far as to separate families on this single character, "J-positive" referring to bluing by iodine, "J-negative" signifying no reaction. The bluing of ascus with iodine solution is believed to be due to the presence of an amyloid substance which probably is related to "isolichenin" purified from some lichens. We tested every Discomycete species collected by us and have found it to be a very valuable taxonomic character. Positive bluing with iodine solution may be indicated in the following way and may be of varying intensity:

a. The bluing may be confined to the ascus tip and in the form of a denser area just below the ascostome as observed in some species of *Peziza* St. Amans and *Plicaria* Fuckel.
b. The bluing may be diffused throughout the ascus or most part of the ascus but more intense near the tip, as observed in some collections of *Verpa conica* Swartz *ex* Persoon.
c. The bluing may be confined to the ascostome or plug, or diffuse near the ascus tip but more intense in the pore or plug. (Fig. 138.)

Our observations indicate that the intensity of reaction may also vary according to the age of asci and treatment of the material prior to testing with iodine solution. Many species of Sclerotiniaceae and Geoglossaceae will give an intense reaction with iodine when the ascospores are still inside the ascus but this intensity may decrease with the age or even some asci from the same apothecium may not give any bluing at all. In many cases the tips of young asci will give a quite different reaction and will not blue while asci from the same apothecium after a few days will give a typical iodine reaction. This bluing may again be of weaker intensity or even lacking from asci which have shot out their ascospores. Some members of the family Sclerotiniaceae lose the intensity of bluing with iodine solution after prolonged storage in fixatives containing acetic acid. Likewise, processing of dry material prior to microscopic examination in potassium hydroxide may reduce the intensity of reaction.

The ascospores

The Discomycetes, like most other fungi, have spores with a distinct exo- and endospore membrane. The ascospore size and shape are quite variable. In general, the ascospores in the operculate

series are larger and comparatively broader than those of the inoperculate series. As mentioned elsewhere, the espispore ornamentation is of considerable taxonomic value in the Pezizales. This ornamentation may be small bands or striations on or inside the espispore, or the latter may be studded with small warts, spines, or reticulations. The genera *Cookeina, Phillipsia, Wynnea* Thaxter have longitudinally striated ascospores while the spores of *Leotia* and *Mitrula* spp. give a banded appearance due to the presence of transverse striations (figs. 131, 132). Many species of *Ascobolus* Persoon *ex* Fries have similar striations but the nature of these striations and reticulations is quite different from those mentioned above. Other kinds of espispore markings are found in many genera and have been used to differentiate species. The ascospore size is being used to separate species and within certain limits appears to be constant for a particular species.

The paraphyses

The paraphyses in Discomycetes appear to be morphologically distinct from those present in the Basidiomycetes. Development of these structures precedes ascus initiation and maturation. They are thus believed to be protective in function. Most of the paraphyses arise from the subhymenium along with the asci and are presumably of haploid nature. They are densely filled with proteinaceous granules which often disappear on maturity. The pigmentation of the hymenium is almost entirely localized in the upper half of the paraphyses.

The paraphyses may be branched or unbranched, hyaline or colored and vary considerably in their shape and size. As to their shape, they may be lanceolate as in *Dasyscyphus,* may end as small seta-like structures, as in *Desmazierella,* or may be club shaped as in many species of *Peziza, Plicaria* or *Ascophanus* Boudier. The paraphyses may be monilioid or catenulate as in *Orbilia* Fries and many members of the family Geoglossaceae. Usually the paraphyses are straight but may be hooked or curved near the apex as in case of *Pulvinula* Boudier and *Otidea* Fuckel. Sometimes the paraphyses may stain greenish in iodine solution as in case of *Pithya* Fuckel, *Pseudopithyella, Phillipsia* and many species of *Aleuria* Fuckel. This reaction seems to be of some taxonomic importance as is the presence or absence of carotenoid pigmentation usually tested by mounting the material in a drop of concentrated sulphuric acid. The bluing of paraphyses or the presence of blue colored granules is supposed to indicate the presence of carotenoid pigments.

Sexual reproduction and conidial or imperfect stages in Discomycetes

We ourselves have not worked with any Discomycete with a view to study the sexual cycle in detail. *Pyronema confluens* (Persoon) Tulasne, an operculate discomycete, has served as "a typical" example for the sexual cycle in ascomycetes in many textbooks on mycology. The life cycle in this fungus is undoubtedly well-known although this does not serve as a typical example for even the Discomycetes. Seaver (1928) reviewed the structure and fusion of sex organs and the subsequent development of ascogonium or archicarp in many Discomycetes. One of the most recent reviews of older literature on the subject was made by Rosinski[7] (1956) who described the sexual cycle in *Anthracobia melaloma* (Alb. & Schw. ex Pers.) Boudier in detail.

Imperfect stages in the Discomycetes are not as uncommon as one is led to believe in many treatises. Professor Korf (unpublished) and the authors make a practice of obtaining ascospore shootings from the apothecia of the family Sclerotiniaceae and Helotiaceae for observing the imperfect stages obtained from germinating spores. The presence or absence of conidial stages is of considerable value in indicating the relationships of various forms. Some species of the form genera *Botrytis* Persoon *ex* Fries and *Monilia* Persoon *ex* Fries are the imperfect stages of the pathogenic genera *Botryotinia* Whetzel and *Monilinia* Honey, respectively. *Ascobolus carbonaria* Karsten, from India, was noticed to have *Botrytis* type of conidia while other species of *Ascobolus* are known to form chlamydospores, oidia and small bulbils. Some species of *Peziza* are known to have the form genus *Oedocephalum* Preuss as their imperfect stage as observed by Korf (personal communication).

CLASSIFICATION OF DISCOMYCETES

The system of classifying Discomycetes adapted in this work was essentially proposed by Nannfeldt (1932) and modified by Le Gal (1953). Madame Le Gal recognizes the following six families for the operculate Discomycetes: Ascobolaceae, Helvellaceae, Humariaceae, Morchellaceae, Pezizaceae and Sarcoscyphaceae. We recognize only three families grouped under the order Pezizales merging Ascobolaceae and Humariaceae with Pezizaceae; the family Morchellaceae with Helvellaceae, and follow her concept as far as the family Sarcoscyphaceae is concerned. The inoperculate Discomycetes are arranged according to the system proposed by Nannfeldt

7. Rosinski, Martin A. 1956 Development of the ascocarp of *Anthracobia melaloma*. Mycologia 48: 506-533.

(1932) and modified by Fitzpatrick and Korf (unpublished). The latter authors recognize the following six families for the inoperculate Discomycetes: Dermateaceae, Geoglossaceae, Helotiaceae, Hyaloscyphaceae, Orbiliaceae and Sclerotiniaceae.

A KEY TO THE ORDERS AND FAMILIES OF DISCOMYCETES

I. Asci operculate, ascopores unicellular ... Order Pezizales a. (p. 124)
  a. Apothecia stipitate, pileus variously shaped ... Helvellacae (p. 125)
  a. Apothecia sessile or rarely stipitate, apothecial disc cupulate: ... b.
  b. Apothecia usually bright-colored, stipitate, lignicolous, ectal excipulum of textura intricata. ... Sarcoscyphaceae (p. 126)
  b. Apothecia variously colored, usually sessile, ectal excipulum of tissues other than textura intricata ... Pezizaceae (p. 126)

I. Asci inoperculate, ascospores uni-, bi-, or multi-cellular:
  A. Ascospores acicular or thread-like, asci elongate-cylindrical, abruptly tapering below into a short narrow base, Order Ostropales (not known to the authors from India)
  A. Ascospores not acicular or thread-like, asci cylindrical, gradually tapering below into a somewhat elongate narrow base: ... Order Helotiales a. (p. 127)
  a. Apothecia arising from sclerotia formed in the host-tissue or from stromatized host-tissue ... Sclerotiniaceae (p. 127)
  a. Apothecia not arising from sclerotia or stromatized host-tissue: ... b.
  b. Ascoma terete, spathulate or mitrate, stipitate, terricolous, Geoglossaceae (p. 127)
  b. Ascoma cupulate, foliicolous or lignicolous: ... c.
  c. Apothecia translucent or appearing waxy, paraphyses abruptly swollen ... Orbiliaceae (p. 128)
  c. Apothecia otherwise, paraphyses not abruptly swollen: d.
  d. Ectal excipulum of dark-walled textura globulosa, Dermateaceae (p. 128)
  d. Ectal excipulum of textura prismatica or textura angularis: ... e.
  e. Apothecia hairy or tomentose, usually hyaline or bright-colored ... Hyaloscyphaceae (p. 128)
  e. Apothecia not hairy, variously colored, Helotiaceae (p. 128)

Order Pezizales

Mostly saprophytes; *apothecia* terricolous, humicolous, fimicolous or rarely lignicolous; *hymenium* mostly brightly colored, varying from dirty white, pale yellow to orange-red or from pink to bright or brownish-red; *asci* and paraphyses either lining a cupulate receptacle which may be sessile to subsessile or sometimes stipitate as in Pezizaceae or lining a columnar and alveolate or saddle-shaped to gyrose receptacle; *ascospores* usually ellipsoid or sometimes

globose, unicellular and often marked with callose-pectose ornamentations varying from small warts or spines to reticulations.

Family Helvellaceae. Apothecia exclusively terricolous, dull colored, pale yellow to yellowish brown; *hymenium* spread on a columnar or distinctly stipitate receptacle which may be saddle-shaped, campanulate, gyrose, alveolate or rarely cupulate, the alveolate hymenium usually marked with distinct ridges of sterile tissue; *stipe* even, lacunose or distinctly sulcate, ectal excipulum even and smooth or slightly furfuraceous; *asci* cylindrical, somewhat broad, J-negative, 8-spored (2-spored in *Ptychoverpa*), gradually tapering towards the base; *ascospores* ellipsoid, rarely globose, epispore usually smooth, sometimes ornamented with warts or a fine reticulum, ascospores guttulate, guttules 1-3 and located inside, or a large number of small droplets attached to the outside of the spores near the ends; paraphyses usually club-shaped.

The shape, size and color of asci, paraphyses and ascospores are quite similar in the species of *Helvella* (figs. 47-49, 36-38) and *Morchella.* These species, however, can be easily distinguished on the bases of tissue anatomy and external morphology. The tissue structure is by far the most important single microscopic character for the classification of the species of *Helvella.* The genera in the family Helvellaceae are separated on the basis of ascospore shape, external appearance of apothecium and ectal excipulum. *Helvella* and *Morchella* are the two largest genera of the family and are among the most variable of the Discomycetes. The following six genera are reported from India in this work: *Disciotis* Boudier, *Helvella* L. *ex* Fries, *Morchella* Dill. *ex* Fr., *Ptycoverpa* Boudier, *Rhizina* Fries and *Verpa* Swartz. The following key from senior author's paper on comparative studies (in manuscript) in Helvellaceae will serve the purpose of distinguishing various genera:—

A KEY TO THE GENERA OF HELVELLACEAE

1. Ascospores eguttulate but with a collection of small oil globules attached *outside* their end, ectal excipulum not well differentiated and of relatively broad hyphae ..... *Morchelloideae* 2
1. Ascospores guttulate, ectal excipulum usually well differentiated and of relatively small hyphae ..... *Helvelloideae* 5
2. Ascigerous portion campanulate or discoid-scutellate, without sterile ridges 3
2. Ascigerous portion globose, subglobose or conical, interrupted by sterile ridges ..... *Morchella* Dill. *ex* Fr.
3. Pileus campanulate, attached only at the apex of the stipe but free from the latter throughout the remaining distance 4

3. Pileus usually discoid-scutellate or sometimes reflexed and often veined, subsessile ..... *Disciotis* Boudier
4. Hymenium usually even or slightly rugulose, ascospores broadly ellipsoid and with obtuse ends, asci 8-spored ..... *Verpa* Swartz
4. Hymenium longitudinally plicate, ascospores elongate-ellipsoid with acute ends, asci 2-spored ..... *Ptychoverpa* Boudier
5. Ascospores globose and uniguttulate ..... *Helvellella* Imai
5. Ascospores ellipsoid, uni-, bi-, or triguttulate 6
6. Ascospores broadly ellipsoid, uniguttulate, ascigerous portion usually saddle-shaped or cupulate to discoid 7
6. Ascospores narrowly ellipsoid bi- or triguttulate, ascigerous portion cerebriform 8
7. Ascospores with ends abruptly tapering to a point, apothecia cupulate ..... *Macropodia* Boudier
7. Ascospores with obtuse ends, apothecia saddle-shaped, gyrose, or cupulate to discoid ..... *Helvella* L. *ex* Fries
8. Ascospores biguttulate and non-apiculate, *Gyromitra* Fries *non sensu* Boudier
8. Ascospores with a large central and two small guttules, spore wall distinctly reticulate and usually apiculate ..... *Maublancomyces* Herter

Family Sarcoscyphaceae (p. 134). *Apothecia* lignicolous, cupulate or spathulate, stipitate or rarely subsessile, usually tough and not breaking easily, bright red or brown to dark brown; *ectal excipulum* mostly of textura intricata, smooth, tomentose or hairy, hairs occurring individually or arranged in fascicles; *asci* J-negative, comparatively elongate-cylindrical, thick-walled, ascostome apical or eccentric in some genera; *ascospores* smooth or striated but not ornamented with distinct warts, spines or reticulations; paraphyses variable.

The following eight genera out of approximately fifteen are known from India, *Cookeina* Kuntze, *Desmazierella* Libert, *Phillipsia* Berkeley, *Pithya* Fuckel, *Plectania* Fuckel, *Pseudopithyella* Seaver, *Pseudoplectania* Fuckel and *Wynnea* Thaxter.

Family Pezizaceae (p. 135). *Apothecia* usually terricolous, typically cupulate to discoid, sessile or occasionally substipitate to stipitate, brittle or rarely tough and cartilaginous, the ectal excipulum smooth, tomentose or hairy, hairs usually erect and stiff, branched or unbranched, hyaline or variously colored; *asci* typically cylindrical, ascospores variable in number, usually eight, seldom more or less, ascostome usually apical; ascospores hyaline or colored, color varying from pale yellow, violet to light or dark brown; *paraphyses* usually club-shaped, straight or slightly curved or hooked.

Twenty-six genera out of approximately sixty reported for this family are included in the present paper.

Order Helotiales

Apothecia usually lignicolous, parasitic with or without sclerotia, often saprophytic or terricolous; *hymenium* variously colored, usually lining a cupulate to discoid receptacle and thus forming a typical apothecium, or lining a columnar receptacle as in the family Geoglossaceae; *asci* cylindrical to broad-clavate, J-positive or J-negative; *ascospores* septate or unseptate, narrowly ellipsoid to filiform, rarely globose, without epispore ornamentation; paraphyses hyaline or occasionally colored, usually filiform, sometimes lanceolate or monilioid.

There are six families in the order Helotiales and their limits are not as well defined as those of the families in the order Pezizales. These families are: Sclerotiniaceae, Dermateaceae, Hyaloscyphaceae, Geoglossaceae, Helotiaceae and Orbiliaceae.

Family Sclerotiniaceae (p. 147). *Apothecia* stalked, arising from a distinct sclerotium formed in various parts of the host (except in *Coprotinia* Whetzel, which is fimicolous) or from a stromatized portion thereof; hymenium variously colored, and lining a cupulate or discoid receptacle; conidial stages quite common, usually belonging to the form genera *Monilia*, *Botrytis* or *Glocosporium;* spermatia often present and usually formed in phialids; *asci* usually 4-8 spored, cylindrical, J-positive or rarely J-negative; *ascospores* ellipsoid, hyaline or subhyaline, rarely turning brown and becoming septate, sometimes budding microconidia or spermatia.

Family Geoglossaceae (p. 149). *Ascophores* terricolous, stipitate, clavate, spathulate or pileate, variable in size, glabrous, hairy or sometimes gelatinous; *hymenium* spread over a terete or clavate receptacle made up of a core of more or less parallel hyphae forming a medulla or a pileate receptacle with distinct ectal excipulum; *asci* cylindrical to clavate, usually 8-spored, occasionally 2-7 spored, gradually tapering towards a base, J-positive or J-negative; *ascospores* usually ellipsoid, elongate cylindrical and usually narrow, usually multicellular, occasionally unicellular and appearing banded, hyaline to dark brown; *paraphyses* variously shaped and colored.

Seaver (1951) reported ten genera for the family Geoglossaceae from North America north of Mexico. Depending upon the author, there are some 13 to 17 genera in this family. These genera are mainly separated on the basis of general appearance, texture, and color of the ascophore; the color and number of cells in an ascospore; and the presence or absence of setae in the apothecia. The

genera *Cudonia* Fries, *Leotia* Persoon *ex* Fries, *Neocudoniella* Imai and *Sarcoleotia* S. Ito and Imai are mitrate; the genera *Ascocorynium* S. Ito and Imai, *Geoglossum* Persoon *ex* Fries *emend.* Durand, *Gymnomitrula* Imai, *Microglossum* Gillet *emend.* Imai, *Mitrula* Fries *emend.* Imai, *Scleromitrula* Imai, *Spathularia* Persoon *ex* Fries and *Trichoglossum* Boudier are terete or spathulate; and the genus *Hemiglossum* Patouillard is coralloid. The terete or spathulate forms of apothecia are modifications of discoid or cupulate apothecial initials and morphologically are not far removed from them.

Family Orbiliaceae (p. 151). Saprophytes (usually lignicolous); *apothecia* sessile or short-stipitate, soft and fleshy, translucent; *hymenium* subhyaline to pale yellow or occasionally pinkish to red; *ectal excipulum* of textura globulosa or of textura prismatica; *asci* usually small, not more than 40-50 μ long, cylindrical and with a truncate apex; *ascospores* hyaline, unseptate; paraphyses hyaline, filiform and with globose to subglobose apices.

There are only three genera, *Patinella* Saccardo, *Orbilia* Fries, and *Hyalinia* Boudier, in this family. Only *Orbilia* and *Hyalinia* are reported from India.

Family Dermateaceae (p. 148.) Parasites or saprophytes; *apothecia* erumpent or sessile, usually dark, sometimes yellowish or of reddish tint, cartilaginous, leathery or fleshy; *ectal excipulum* of dark-walled textura globulosa; *asci* variable in shape and size, J-positive or J-negative; *ascospores* hyaline to brown, septate or unseptate; *paraphyses* variable.

Depending upon the author, between 40-60 genera are recognized for this family and these are arranged in eight or nine tribes. Only two genera are reported from India in this paper.

Family Hyaloscyphaceae (p. 149). Saprophytes; *apothecia* sessile to distinctly stipitate, usually bright colored, hairy; *hairs* hyaline or colored, frequently ornamented with small warts; *ectal excipulum* of textura prismatica or rarely of textura globulosa; *hymenium* hyaline, pink, golden yellow or sometimes reddish; *asci* clavate, usually staining blue with iodine solution; *ascospores* hyaline, ellipsoid, septate or unseptate; *paraphyses* filiform to lanceolate.

There are 16 genera reported for this family and the following three are known from India: *Dasyscyphus* S. F. Gray, *Dasyscyphella* Tranzschel and *Arachnopeziza* Fuckel.

Family Helotiaceae (p. 151). Saprophytes or parasites; *apothecia* usually bright colored, sessile or distinctly stipitate; *ectal excipulum*

of textura intricata or of textura prismatica; *hymenium* variously colored, usually not very thick; *asci* cylindrical to clavate, J-positive or J-negative; ascospores ellipsoid, hyaline to pale yellow or light to dark brown, unseptate or septate; *paraphyses* variable.

This family is an assemblage of a large number of genera of doubtful relationship. The writers have an extensive collection of Discomycetes belonging to this family but have not worked with them.

MATERIALS AND METHODS

Most of the fungi reported in this paper were collected from various localities in the North Western Himalayas within the limits of the temperate zone and included within 76.0 to 79.0 E. longitude and 28.0 to 32.0 N. latitude. This area includes the hill stations of Sat Tal, Bhim Tal, and Naini Tal in Kumaon Hills (altitude 5,000-9,000 ft.); Dehra Dun and Hardwar in Shiwalik Hills (altitude 1,800-3,000 ft.); Mussoorie, Rajpura and their suburbs in Mussoorie Hills (altitude 4,500-8,000 ft.); Srinagar, Pahalgam and Amarnath Temple in Kashmir (altitude 5,000-18,000 ft.); and Dalhousie in Panjab Hills (altitude 5,000-7,000 ft.).

It is characterized essentially by a monsoon climate. During the span between June and August, the forests are wrapped in clouds and the air is saturated. Almost 60 to 80 percent of the annual precipitation falls within this period. There is considerable cloudiness in the winter and about 20 to 30 percent of the annual precipitation falls in the form of snow. Spring and autumn are pleasant and sunny. The best period for collection of fungi, the Discomycetes in particular, is from the first week of August through the last week of September.

An outline map of India showing principal stations in the collecting areas mentioned in the text. Stippled areas indicate the mountains. (Approximate scale: One inch = 250 miles.)

Range of distribution, the location of herbarium, and listing of collections

We have attempted to list the representative areas in which we have personally collected the material. Wherever possible, the range of distribution for each species is also given. This does not mean that a particular form does not occur elsewhere, or that it will always be found in the area given. The abbreviation at the end of the listing of a species is that of the herbarium where the specimen is located. Most of the material pertaining to the operculate Discomycetes is deposited in the Panjab University Herbarium, Chandigarh, India, and the specimens are designated by the same numbers as published by Thind and his students (1957, a, b, c, and d). The remaining material is deposited in the Herbarium, Department of Plant Pathology, Cornell University, Ithaca, New York, U. S. A.

Abundance

How often a particular species has been collected or how many specimens are usually collected at one time, *i. e.*, the abundance, is estimated and therefore relative. It is indicated in the following way: If several specimens of a species have been collected at one time, and the fungus has been collected often, the term "abundant" is used; and the terms "common," "uncommon," and "rare" are used for decreasing abundance.

The substratum, which is usually considered as important in classification at the species level in some genera, is indicated in each case.

Collection and preservation of Discomycetes

The best areas for the collection of material are damp and moist places along the banks of streams or other bodies of water. The forest floors under deciduous trees and conifers in Himalayas are ideal places to search for this kind of material. Some of the species which occur on the plains during winter are found in early spring or summer in the mountains. Some early summer species of the lower altitudes can be easily found at higher altitudes in mid- or late summer. Thus while the apothecia of the members of the family Sclerotiniaceae are usually found in winter in the Panjab plains, the same are found in early spring at lower altitudes or late in summer at the higher altitudes. Although apothecia of most of the Pezizales and Helotiales are ephemeral and it is not uncommon to find a sudden absence of a species from familiar places in a particular locality, other species will undoubtedly be found in the same area and some species can be found throughout the year.

The Discomycetes can be easily collected in small paper bags and stacked in small cardboard boxes in a suitable basket or a bag. Immediate preservation of specimens in liquid media not only deprives one of the examination of fresh material in the laboratory but sometimes makes it impossible to determine the correct name for a fungus. Field notes were preferably taken at the time of collection, as many forms will change color on bruising or during transportation to the camp.

Preparation for microscopic examination

All material (except for the following) was examined in fresh condition. These exceptions are: *Wynnea macrotis* (Berk.) Berk., *Peziza repanda* Pers., *Humaria palidisetosa* Cash, *Humarina cacaina* Thind, Cash and Sethi, *Ptychoverpa bohemica* (Krombh.) Schröt., *Monilinia fructicola* (Winter) Honey, *Botryotinia ricini* (Godfrey) Whetzel, *Pseudopeziza medicaginis* (Lib.) Sacc., *P. repanda* (Fr.) Karst, *P. trifolii* (Biv.-Bern.) Fuckel.

The dried specimens were "revived" by soaking in two percent aqueous solution of potassium hydroxide for one to two hours before staining for the study of detailed apothecial anatomy and epispore markings. The free-hand sections, or sections made with a freezing microtome were stained in one percent aqueous phloxine solution for one to two minutes and mounted in slightly acidified 50 percent aqueous glycerine for routine examination. Some sections were also mounted directly in lactophenol or stained in Cotton Blue in lactic acid and then mounted in lactophenol. As mentioned elsewhere, the epispore ornamentation is of considerable taxonomic value at the species level. Unstained preparations of ascospores give a very erroneous picture of the true nature of the spore markings. The Cotton Blue Staining Technique used by Madam Le Gal of France is indispensable for the study of epispore ornamentation. The batch of Cotton Blue dye used makes a considerable difference in the intensity of coloring imparted to the ornamentation. The Cotton Blue C4B of the Allied Chemicals Corporation of New York gave much better results than other Cotton Blue dyes tested by us. The staining solution is prepared as follows: Fifty mg of the dye are dissolved in 30 ml of lactic acid, allowed to stay at room temperature for two to four days and then filtered. Thin sections of hymenium or small fragments from revived material are mounted in a small drop of this stain, a cover slip added and the slide warmed over a small flame till the staining solution just begins to boil. The epispore ornamentation stains blue to deep blue

while the remaining spore wall does not stain appreciably. Cotton Blue also stains the cytoplasm, and the septa of paraphyses and ascospores if any, can be easily demonstrated.

Staining of asci for the Iodine Test is accomplished likewise in iodine solution, frequently referred to as Meltzer's Reagent. Meltzer's Reagent is prepared by dissolving 1.5 gm of potassium iodide, 0.5 gm of iodine crystals and 20 grams of chloral hydrate in 20 ml of distilled water. Although many workers in Discomycete taxonomy use this solution as such, we have preferred to dilute the solution to half its original strength without any loss of intensity of bluing reaction, thus eliminating the undesirable dark brown background which somewhat obstructs the view through the microscope. Iodine solution also gives a dark yellowish-brown color to the walls of spores, paraphyses and some hyphae, and septa in these structures, when present, become distinct. We made a practice of examining all freshly collected material mounted in water for observing the color and taking measurements of asci, ascospores and paraphyses. Free-hand sections were made where possible and examined as mentioned below.

While there are several methods of preserving and storing small and brittle fungi occurring on fragile substrata such as soil, rotten wood or decayed leaves, we found it useful to process our specimens before transportation in the following way: Pieces of fragile substrate of suitable sizes were placed on a blotting paper with the specimen side facing downward. A 40 percent solution of commercial gum arabic prepared in five percent aqueous solution of copper sulphate was added drop-wise until the solution just soaked through the entire substratum. The material was then placed in a drying oven at 50° C, or in a home-made dryer made out of a wooden box fitted with electric or kerosene lamps. Every four to six hours a few drops of gum solution were added until the entire substratum was soaked, and allowed to dry thoroughly before packing, storing and shipping. The above method not only prevents the breaking of apothecia during shipment but saves considerable time in the field sorting individual specimens. It also avoids the sometimes futile search for small apothecia dislodged from the substratum during transit or handling.

This method of processing the specimens may not be useful during the months of monsoon unless a good drying mechanism is at hand. Copper sulphate inhibits the superficial mold growth and after processing, the specimens should be stored in a dry place.

The material for cytological details was fixed in formalin-acetic alcohol or Carnoy's solution and stored in 50 percent ethanol.

The identifications were made with the help of Seaver's monographs, The North American Cup-fungi. Such identifications were later checked by comparing the material with authentic specimens in the Herbarium of the Department of Plant Pathology, Cornell University, or on loan from other herbaria through the courtesy of Dr. Richard P. Korf, Curator of the Herbarium. Several experts were consulted on special problems and their opinions are incorporated. A detailed study of some taxa was not possible by the authors at this stage. The name used by Seaver (1928, 1951) or other workers was adopted in such cases, as is indicated by the use of the term "*sensu* Seaver."

PART I

OPERCULATE DISCOMYCETES

Family CYTTARIACEAE (not reported from India).

There is only one genus, *Cyttaria*, with a number of species parasitic on *Nothofagus* in the southern hemisphere (Australia, Tasmania, New Zealand, Chile, and Argentina).

Family SARCOSCYPHACEAE

COOKEINA O. Kuntze.

* *C. sulcipes* (Berk.) Kuntze, on rotten wood of gymnosperms, Jumna Bridge near Mussoorie, August, uncommon. CUP-I 1 = LRB 150.

C. venezuelae (Berk. & Curt.) Le Gal, described as "*Cookeina colensi* (Berk.) Seaver" by Thind & Batra (*62*: 436), on rotting wood of *Delbergia* sp., Kansro, near Dehra Dun, uncommon, mid-August to September. PUI-160; BPI.

PHILLIPSIA Berk.

P. Domingensis Berk. described as *P. gigantea* Seaver by Thind & Batra (59: 53), on logs of woody angiosperms, Kansro, near Dehra Dun, mid-August to mid-September, common in some years. PUI-126; BPI.

PITHYA Fuckel.

P. cupressina Fuckel, published as *P. cupressi* (Batsch) Rehm by Thind & Batra (1957), on dead "needles" (branches) of *Cupressus* spp., Cemetery, Camel's Back Road, Mussoorie, August to September, common, (*6*: 28; *62*: 430). PUI-155; BPI; CUP-I 2 = LRB 163.

PLECTANIA Fuckel.

* *P. floccosa* (Schw.) Seaver, on rotting twigs of *Quercus incana*, common, August to September. PUI = CUP.

* *P. nannfeldtii* Korf = *Paxina nigrella* Seaver, on rotting wood, Jabber Khet, Mussoorie, September, uncommon, (*6*: 101, 102). PUI.

PSEUDOPITHYELLA Seaver.

P. miniscula (Boud. & Torrend) Seaver, on dead "needles" (branches) of *Cupressus* spp., Cemetery, Camel's Back Road, Mussoorie, August to September, common, (*6*: 71, 72). PUI; CUP-I 3, and 197 = LRB 143 and 919, respectively.

PSEUDOPLECTANIA Fuckel.

* *P. nigrella* (Pers.) Fuckel, on rotting twigs or stumps of angiosperms, Dhobi Ghat, Mussoorie; also from Siri Nagar (Kashmir), August to September, uncommon. CUP-I 4 = LRB 102.

WYNNEA Berk. & Curt. in Berk.

W. americana Thaxter, Lal Tibba, Mussoorie, September, rare, (*6*: 91; *59*: 51). PUI-125; CUP-I 5 = LRB; BPI.

W. macrotis (Berk.) Berk., on rotten wood, Darjeeling, (*16*: 203; *18*: 424; *20*: 12; *23*: 30; *40*: 934; *41*: 1307; *51*: 547). CUP-D.

Family PEZIZACEAE

ALEURIA Fuckel (*non Aleuria* [Fr.] Boud.).

A. aurantia (Pers. *ex* Fr.) Fuckel, on soil, Jabber Khet, Mussoorie; Sikkim, August, uncommon, (*6*: 36; *16*: 203; *20*: 12; *24*: 109; *31*: 128; *62*: 434). PUI-158 = BPI; K.

A. *rhenana* Fuckel, on soil (*64*: 228). PUI-302 to 304.

**A. rubra* Batra, *Apothecia* gregarious, sessile, firmly attached to soil, cupulate or more often discoid at maturity; *discs* "Vivid Red" [8] when fresh, fading on drying, externally hairy, 2-6 cm in diameter; *rooting hairs* absent; *superficial hairs* present, abundant, scattered all over the outer surface, denser towards the margin, hairs deciduous, unbranched, septate, usually curved, dark brown, adpressed to the apothecium, 200-300 x 9-11 μ, much smaller near the margin. *IN SECTION: hymenium* orange-red due to pigmentation in the paraphyses, 256-300 μ thick; *hypothecium* "subhymenium" light orange, of a compact textura intricata, 60-70 μ; *medullary excipulum* less compact but otherwise similar to hypothecium, 310-330 μ; *ectal excipulum* 2-5 layers of large cells of textura angularis interspersed with some hypha-like cells giving rise to unbranched hairs, 160-180

8. Colors in quotation marks are taken from: Ridgeway, R. 1912. Color Standards and Color Nomenclature. Pp. 43, Pl. 43, Washington, D. C.

μ; *asci* cylindrical, 8-spored, attenuate towards the base, rounded at the apex, operculate, J-negative, (250-) 300-330 x 10-12 μ; *ascospores* ellipsoid, subhyaline, sculptured, sculpturing consisting of warts which form a distinct and conspicuous reticulum, the two polar warts very large, thick and forming two apiculi, (18-) 24-26 (-28) x 10-13 μ inclusive of ornamentations; *paraphyses* cylindrical, orange colored, usually branched, swollen at the tips, 310-340 × 2-3 μ, reaching up to 9 μ at their extreme tips (Fig. 14-16).

Cultural characters: Ascospores germinating within 24-36 hrs. on potato-dextrose agar, mycelium scanty, mostly intramatrical, hyphae septate, hyaline, frequently anastomosing, imperfect stage unknown.

Substratum: soil.

Name: rubra, red; after the hymenium color.

Type locality: Municipal Gardens, Mussoorie, (U. P.) India.

Type specimens: Holotype, Cornell University (CUP-I 6 = LRB 141); Isotype, Botany Department, Panjab University, India.

Illustrations: Mycologia 52: 525, figs. 1-3.

Specimens examined: from the above-mentioned range of distribution, CUP-I 188 = LRB 1003.

A. rutilans (Fries) Gill., on soil or living mosses, usually *Mnium heterophyllum,* Jabber Khet, Mussoorie, Dalhousie and Siri Nagar (Kashmir), July to September, common, (*6:* 39; *20:* 11; *31:* 128; *62:* 435). PUI-159; BPI; K; CUP-I 60 = LRB 184.

ANTHRACOBIA Boud.

* *A. melaloma* (Alb. & Schw. *ex* Fr.). Boud., on recently burnt places, widely distributed throughout North Western Himalayas, August to September, common. PUI; CUP-I 7 = LRB 101.

ASCOBOLUS Pers. *ex* Fr.

A. carbonarius Karst., on charcoal and burnt soil, Municipal Garden, Mussoorie, Dalhousie and Siri Nagar (Kashmir), July to August, common, (*6:* 31; *62:* 432). PUI-157; BPI. CUP-I 63 = LRB 169.

* *A. furfuraceous* Pers. *ex* Fr., human excreta and cow dung, Chola Sahib, Dist. Amritsar, August to October (sometimes to November), common. PUI; CUP-I 8 = LRB 138.

* *A. geophilus* Seaver, on soil, Mussoorie, August to September, common. CUP-I 201 = LRB 963.

A. glaber Pers. *ex* Fr. on rabbit dung, Amritsar and Rohtak, Panjab, (*1:* 11). PUI; Ahmad-808.

A. immersus Pers. *ex* Fr., from all localities around Mussoorie, Dalhousie and Siri Nagar (Kashmir), on cow dung, July to September. The ascospores in the form reported from these areas are in the range of (40-) 50-60 x (27-) 30 μ, and the spore sculpturing of "sparse reticulations" (*54*: 83) is rarely observed, (*52*: 198). PUI; DU.

A. magnificus B. O. Dodge, on cow dung, Jumna Bridge near Mussoorie, and Dehra Dun, July to August, uncommon, (*6*: 30, 31; *48*: 8; *62*: 432). PUI-156 = BPI; Ahmad 604; CUP-I 58 = LRB 166.

ASCOPHANUS Boud.

This genus comprises an assemblage of various unrelated forms inhabiting various kinds of dung or barnyard manure. The asci of some species are J-positive while some others are J-negative. Future work will probably necessitate removing J-positive forms from this genus.

**A. glaucellus* Rehm., on cow dung, Dhobi Ghat and other localities around Mussoorie, August to September, uncommon, (*6*: 56). PUI; CUP-I 9 = LRB 130.

**A. granulatus* (Bull. *ex* Fr.) Spegz., on cow dung and barnyard manure, The Park, Mussoorie, September, uncommon, (*6*: 49, 50). CUP-I 10 = LRB 149.

**A. holmskjoldii* E. C. Hansen, on cow dung, Dhobi Ghat, Mussoorie; Dalhousie and Siri Nagar (Kashmir), July to September, common, (*6*: 46-48). PUI; CUP-I 11 = LRB 129.

**A. ochraceous* (Crouan) Boud., on dung of various kinds and human excreta, very widely distributed, throughout the North Western Himalayas and Panjab Plains, abundant, (*6*: 54-56). PUI; CUP-I 12 = LRB 128.

A. striatus Thind, Cash & Singh, on cow dung, August. (*6*: 51; *65*: 461). PUI 308.

CHEILYMENIA Boud.

**C. coprinaria* (Cooke) Boud., on cow dung, Dhobi Ghat, Mussoorie, August to September, common. PUI; CUP-I 13.

**C. pulcherrima* (Crouan) Boud., on cow dung, The Park, Mussoorie, August, uncommon, (*1*: 11; *6*: 84). PUI; Ahmad-1821.

C. stercorea (Pers. *ex* Fr.) Boud., on cow dung (*6*: 85; *64*: 223). PUI 299.

* *C. theleboloides* (Alb. & Schw. *ex* Fr.) Boud., on cow dung, Dhobi Ghat, Mussoorie, common, (*6*: 82). PUI; CUP-I 14.

DESMAZIERELLA Libert.

* *D. acicola* Libert, on pine needles, July and August, common throughout lower altitudes (5,000-7,000 ft.) in Himalayas. CUP-I 192 = LRB 923.

DISCINA Fries.

* *D. leucoxantha* Bres., on soil, apothecia 3-10(-13) cm, hymenium yellow to brownish yellow, Dalhousie, September, rare. PUI; CUP-I 15 = LRB 119.

GEOPYXIS (Pers.) Sacc.

* *G. vulcanalis* (Peck) Sacc., *Humarina ochroleuca* (Clements) Seaver, *sensu* Seaver (1928), on soil, Lal Tibba, Mussoorie, Dalhousie, August to September, uncommon, (*6*: 66). PUI; CUP-I 59 and CUP-I 190, 191 = LRB 876 and 983, respectively.

HUMARIA Fuckel.

* *H. ahmadii* Cash, apothecia 1-3 mm, hymenium "bright red," on soil, Delhi, (type locality Lahore, Pakistan), September, rare. PUI.

H. hemispherica Weber *ex* Fr., on soil, Camel's Back Road and other localities around Mussoorie, Dalhousie, Siri Nagar (Kashmir), August to September, common, (*6*: 86, 87; *60*: 204). PUI-141, 142 = BPI; CUP-I 16, 187 = LRB 99 and 1128, respectively.

H. pallidisetosa Cash, apothecia 6-8 mm, hymenium "wood brown to drab," on ground, Rohtak, January, known only from the type locality, (*21*: 725). BPI; Ahmad-1776.

H. subreticulata Thind, Cash & Singh, on soil, August, (*65*: 459). PUI-307 = BPI.

HUMARINA Seaver.

As in the case of *Ascophanus*, this genus is also an assemblage of unrelated forms. Some of the forms described under this genus can certainly be referred to some of the older genera. The remaining forms whose authentic material was not available at present are listed under *Humarina sensu* Seaver.

H. axillaris (Nees *ex* Fr.) Seaver *sensu* Seaver, on soil, Mussoorie, (*54*: 124). CUP-I 17 = LRB 151.

H. cacaina Thind, Cash and Sethi, on soil, Woodstock School, Mussoorie, (63: 833). PUI-162 (type); BPI. (See also p. 167).

* *H. convexula* (Pers. *ex* Fr.) Seaver *sensu* Seaver, on soil among mosses, Kincraig, Mussoorie, August, uncommon, (*6*: 60). PUI; CUP-I 61 = LRB 179. (See also p. 167).

* *H. semiimmersa* (Karst.) Seaver *sensu* Seaver, burnt places, Jabber Khet, Mussoorie, August to September, common (*6*: 63). PUI; CUP-I 64 = LRB 196.

JAFNEA Korf.

* *J. fusicarpa* (Ger.) Korf, on soil, August, Lal Tibba, Mussoorie, PUI; CUP-I 18 = LRB 120.

LAMPROSPORA de Not.

* *Lamprospora chopraiana* Batra, Mycologia 52: 665. 1960. (This paper fig. 7, 8.) *Apothecia* cupulate, becoming discoid on maturity, scattered; *disc* with a minutely crenulate margin, 2-4 mm broad, 1-1.5 mm high, "Sanford Brown" to "Amber Brown," turning "Madder Brown" on maturity, flesh not changing color on breaking; *IN SECTION:* hymenium 230-250 μ thick, light brown due to pigmentation in paraphyses; *subhymenium* and *medullary excipulum* indistinguishable, together measuring 120-160 μ thick, of textura intricata, hyphae subhyaline, 4-5 μ broad; *ectal excipulum* 80-120 μ thick, of textura globulosa, some cells of the outermost layer elongate and hairlike, inner layers exclusively of textura globulosa whose cells measure 15-30 x 10-25 μ; *asci* operculate, cylindrical, 8-spored, abruptly tapering below into a short stem-like base, J-negative, 200-240 x 15-18 μ; *ascospores* globose, arranged uniseriately, hyaline, smooth walled, with a large guttule almost filling the spore, (11-) 14-17 μ; paraphyses unbranched, septate, brownish, of the same size as asci, 3-4 μ broad, not curved at the apex, where they are slightly swollen and measure 4-5 μ.

Cultural characters: unknown.

Habitat: Cupressus branches, "needles."

Name: After Professor Ram Saran Chopra of Botany Department, Panjab University, India.

Type locality: Cemetery. Camel's Back Road, Mussoorie, Uttar Pradesh, India.

Type specimen: Cornell University (CUP-I 73 = LRB 142), Collected on August 4, 1952 along with *Pseudopithyella miniscula* (Boud. & Torrend) Seaver.

Illustrations: Mycologia 52: 666, figs. 4 and 5.

Distribution: Known only from the type locality and collected by L. R. Batra during the years 1954, 1955, and 1960.

There does not appear to be any globose-spored operculate Discomycete with brown apothecia, hyaline and smooth spores, characteristic of *Lamprospora chopraiana*. *Lamprospora leiocarpa* (Curr.) Seaver has a superficial resemblance with this fungus in young condition but the apothecia of the former reach a diam. of 2-3 cm. These two fungi, however, are different microscopically.

* *Lamprospora multiguttula* Batra, *Mycologia* 52: 665. 1960. (This paper fig. 4-6.) *Apothecia* gregarious, sessile, fragile; *disc* shallow cupulate or saucer-shaped, with an entire margin, 2-3 mm in diam., "Orange Chrome" to "Cadmium Orange;" *IN SECTION: hymenium* orange colored, 200-220 μ thick; *subhymenium* inconspicuous, 30-40 μ thick, of textura intricata, hyphae subhyaline; *medullary excipulum* of textura intricata, 50-60 μ thick, hyphae 2-3 μ in diam.; *ectal excipulum* conspicuous, of compact textura intricata, 28-36 μ thick, tips of most hyphae oriented outwards, hyphae 2-3 μ in diam., with tips reaching up to 4-5 μ; *asci* cylindrical, 8-spored, gradually tapering towards the base and rounded at the apex, J-negative, 210-240 (290) x 14-19 μ; *ascospores* perfectly globose, uniseriate, hyaline, smooth walled, containing 5-9 guttules, ascospores 12-13 (14) μ in diam.; paraphyses unbranched, septate, orange colored, 200-240 x 2-3 μ, reaching up to 4 μ at the tips.

Cultural characters: unknown.

Substratum: soil.

Name: Multi ex Latin = many, *guttula ex* Latin = small drops.

Type locality: Mussoorie, Uttar Pradesh, India.

Type specimen: Holotype, Cornell University (CUP-I 104 = LRB 1176); paratype University of Kansas, collected by the author during August, 1954.

Illustrations: Mycologia 52: 666, figs. 1-3.

Specimens examined: three different collections from the type locality only.

* *L. planchonis* (Dun.) Seaver, on soil, Jabber Khet, Mussoorie, PUI; CUP-I 20 = LRB 171.

L. spinulosa Seaver, on soil, widely distributed around Mussoorie, August, common, (*6*: 19; *62*: 428). PUI 153 = BPI; CUP-I 21 = LRB 100.

LASIOBOLUS Sacc.

* *L. equinus* (Mull.) Karst., on cow and horse dung, Kempty Falls and other localities around Mussoorie, July to September, common. PUI; CUP-I 23 = LRB 152.

PEZIZA L. *ex* Fr.

P. badio-confusa Korf = *P. badia* Pers. *sensu* Seaver, on burnt places and charcoal, Jabber Khet, Mussoorie; Dalhousie, August to September, very common, (*6*: 109, 110; *48*: 8; *59*: 57). PUI-129; BPI. Korf (pers. comm.) thinks this fungus is not *P. badio-confusa* Korf.

P. brunneoatra Desm., on soil, Balharu Khud, Mussoorie, August to mid-September, very common, (*6*: 112, 113; *59*: 57). PUI-130, 131; BPI; CUP-I 24 = LRB 162.

* *P. gerardi* Cooke, on soil, Lal Tibba, Mussoorie, August, uncommon, (*6*: 67). PUI.

* *P. melaleuca* (Bres.) Seaver *sensu* Seaver, on soil, Jabber Khet, Mussoorie, August to September, common, (*6*: 117, 118). PUI.

* *P. melaleucoides* Seaver *sensu* Seaver (1928), on soil, Jabber Khet, Mussoorie, reported also from Dalhousie and Simla, mid-August to mid-September, common, (*5*: 118, 119). PUI.

P. pustulata Pers. *ex* Fr., reported by Thind and his colleagues, on soil, (*61*: 34). PUI-152 = BPI.

P. repanda Pers. *ex* Fr., on rotten wood of angiosperms, Jabber Khet and Park, Mussoorie, mid-August to mid-September, uncommon. PUI.

P. succosa Berk., on soil under pine forests, The Park, Jabber Khet, and other localities in the vicinity of Mussoorie, mid-July to mid-September, common, (*6*: 113, 114; *59*: 59). PUI-132 = BPI, CUP-I 195 and 196 = LRB 1142 and 1149, respectively.

* *P. vesiculosa* Bull. *ex* Fr., on manure piles, Khalsa College, Amritsar, March, rare, (*6*: 124). PUI; BPI.

PLICARIA Fuckel *emend.* Boud. *non emend.* Rehm.

* *Plicaria papillosa* Batra, *Mycologia* 52: 665. 1960. (This paper, Figs. 9, 10.) *Apothecia* cupulate, scattered, sessile, with a crenate margin, 5-10 mm broad, up to 5 mm deep, exteriorly dark brown and strongly tuberculate or papillose, tubercles 150-300 (400) μ high, 120-250 μ broad near the base; *IN SECTION: hymenium* purple brown, 370-400 μ thick; *subhymenium* of textura intricata which is not very conspicuous; *medullary* and *ectal excipulum* indistinguishable, together 311-410 μ, both of textura prismatica whose cells are 25-43 x 11-18 μ, cells of the tubercles slightly larger, being 25-43 x 21-28 μ; *asci* operculate, 8-spored, cylindrical, gradually tapering towards the base, J-positive, 360-380 x 19-21 μ; *ascospores* globose, light brown, uniguttulate, verrucose, ornamentations of small warts, 17-18 (-19) μ; *paraphyses* unbranched, septate, brown, as long as asci, 4-6 μ broad, up to 11 μ near the tip.

Cultural characters: unknown.

Name: Papillosa ex Latin = bearing nipple, referring to the papillose nature of the exterior of the apothecium.

Type locality: Dalhousie, Panjab, India.

Type specimen: Cornell University (CUP-I 72 = LRB 178), collected by the senior author on July 15, 1955.

Illustrations: Mycologia 52: 666, figs. 4 and 5.

Distribution: Dalhousie (Panjab) and Mussoorie (Uttar Pradesh), India.

Specimens examined: from the above localities.

Plicaria papillosa superficially resembles *Peziza endocarpoides* Berkley (Flora Nov. Zeal. *11:* 199, pl. 105; Cooke's Mycographia, fig. 84.) but the latter has much smaller and smooth walled spores. *Peziza atrospora* Fuckel (Cooke, Mycographia, p. 170, pl. 75, fig. 294) and *Peziza scabrosa* Cooke (l. c., fig. 295) have much larger apothecia, with ascospores differing in many ways from that of *Plicaria papillosa.*

* *Plicaria pseudoplanchonis* Batra, Mycologia 52: 667. (This paper, figs. 11-13). Apothecia gregarious or occasionally scattered, sessile or subsessile, cupulate, cups shallow, with a crenate margin, 1-1.2 cm broad, up to 0.5-0.8 cm high, exteriorly purple brown, fleshy, brittle, externally tuberculate, tubercles pyramidal, 36-100 x 21-36 μ; *IN SECTION: hymenium* 350-360 μ thick, brown due to pigmentation in paraphyses; subhymenium not conspicuous, of compact textura intricata, brown; *medullary excipulum* forming the major portion of the apothecial flesh, 300-410 (450) μ thick, of textura intricata, most of the hyphae directed outward, hyphae brown, 1-2 μ broad; *ectal excipulum* 32-40 μ thick, of textura globulosa, dark brown, cells 8-18 x 7-11 μ; *asci* 8-spored, cylindrical, gradually tapering below into a short stem like base, J-positive, 316-360 x 16-20 μ; *ascospores* globose, light brown, occasionally brown, conspicuously sculptured, spore sculpturing consists of spines up to 2-3 μ high, up to 1-1.5 μ broad at the base, uniguttulate, the single guttule almost filling the whole spore on maturity, spores (13-) 15-18 μ in diam. including ornamentations; *paraphyses* unbranched, septate, brown, 350-400 x 3-4 μ, slightly enlarged above, and reaching up to 5 μ in thickness.

Cultural characters: Unknown.

Habitat: On soil under coniferous forest, especially under *Cedrus deodara* L.

Type locality: Cemetery, Camel's Back Road, Mussoorie, Uttar Pradesh, India.

Name: pseudoplanchonis = superficial resemblance to *Lamprospora planchonis* (Dun.) Seaver.

Type specimen: Cornell University (CUP-I 71 = LRB 165), collected by the senior author on August 16, 1952.

Illustrations: *Mycologia* *52:* 666, figs. 8-10.

Distribution: Reported from the type locality in 1952 and 1960 from Dalhousie and Mussoorie (Uttar Pradesh), respectively.

* *P. trachycarpa* (Curr.) Rehm, on burnt places and charcoal, Jabber Khet, Mussoorie, August to September, common, (*6*: 24; *60*: 197). PUI-135 = BPI; CUP-I 22 = LRB 114.

PSILOPEZIA Berk.

* *P. nummularia* Berk., on rotting wood, Jabber Khet, Mussoorie, uncommon. PUI; CUP-I 25 = LRB 115.

PULVINULA Boud.

P. carbonaria (Fuckel) Boud., burnt places, Jabber Khet, Mossy Falls and The Park, Mussoorie, August to September, common, (*6*: 21; *62*: 427). PUI-154; BPI; CUP-I 26, 193, and 194 = LRB 147, 909 and 885, respectively.

* *P. constellatio* Boud., soil, Dhobi Ghat, Mussoorie, Dalhousie and Siri Nagar (Kashmir), August to September, common, (*6*: 22). PUI; CUP-I 27 = LRB 98.

P. discoidea (P. Henn. & E. Nym.) Batra *comb. nov.* (*Basonym; Barlaea discoidea* P. Henn. & E. Nym. Monsunia *1*: 33. 1900), on soil, Mossy Falls, Mussoorie, August, common, PUI; CUP-I 19.

* *P. haematostigma* (Hedw. *ex* Fr.) Boud., Mussoorie, August, uncommon. PUI.

P. mussooriensis (Thind *et al.*) Batra (*Basonym: Lamprospora mussooriensis* Thind, Cash & Singh, Mycologia *51*: 457) on soil, August, common, PUI-306 = BPI.

PYRONEMA Carus.

* *P. omphaloides* (Bull. *ex* Fr.) Fuckel, = *P. confluens* Tul., apothecia 1-2 mm, 2 distinct forms, one with white hymenium and the other with pink, ascospores from each giving rise to the respective parent form in culture, burnt places, Mussoorie, Simla, Dalhousie, Siri Nagar (Kashmir), July to September, abundant, (52: 198). PUI; CUP-I 28.

SACCOBOLUS Boud.

S. kerverni (Crouan) Boud., from all localities around Mussoorie, Dalhousie, Pusa, and Siri Nagar (Kashmir), July to September, abundant, (*6:* 34; *20:* 13; *52:* 205; *56:* 374). PUI; DU; Butler-1356; CUP-I 29 = LRB 152.

SCUTELLINIA (Cooke) Lambotte.

S. *cubensis* (Berk. & Curt.) Le Gal, described as *Humaria cubensis* by Thind & Sethi (1957), on rotting wood and soil, Kempty Falls, Mussoorie, August, common, (*6:* 77-80; *60:* 202). PUI-139; BPI; PUI-140; CUP-I 30.

S. *scutellata* (L. *ex* Fr.) Lambotte, distributed throughout North Western Himalayas and Panjab (India) Hills, July to October, on rotten wood, bark, leaf debris or soil, abundant, (*6:* 76, 81; *52:* 196; *60:* 201). PUI-137, 138; BPI; DU; CUP-I 31 = LRB 175.

*S. *uliginosa* Batra, Mycologia 52: 526. (This paper, figs. 17-20.)

Apothecia gregarious, sessile, discoid; *disc* orange-red when fresh, fading on drying, externally hairy, 2-8 mm (10 mm) in diameter; *rooting hairs* present, abundant, denser towards the margin of the disc, persistent, rarely forked at the base, but otherwise unbranched, non-septate, usually not sharp-pointed, light brown, thick-walled, 150-200 x 10-12 μ; *superficial hairs* present, much smaller in dimension than rooting hairs; *IN SECTION: hymenium* orange-red due to pigmentation in the paraphyses, 250-297 μ thick; *hypothecium* lighter in coloring than hymenium, of compact textura intricata; *medullary excipulum* indistinguishable from hypothecium, both collectively 180-200 μ thick; *ectal excipulum* of 2-4 layers of textura angularis, 68-100 μ; *asci* cylindrical, 8-spored, gradually attenuate towards the base, operculate, J-negative, 220-270 x 12-15 μ; *ascospores* ellipsoid, subhyaline, sculptured, sculpturing consisting of 1-2 μ thick warts, uniguttulate, 20-25 x 11-12 μ including warts; paraphyses unbranched, septate, strongly swollen above, 250-300 x 3 μ, reaching 10 μ at the tips.

Substratum: muddy banks of ponds and swamps.

Name: uliginosus, muddy; after the habitat.

Type locality: Raj Pura, (U. P.), India.

Type specimen: Holotype Cornell University (CUP-I 32 = LRB 145); Isotype: in Botany Department, Panjab University, India.

Illustrations: Mycologia 52: 525, fig. 4-7.

Distribution: the type locality and Pathankote (Panjab), India.

Exsiccati: Korf, Discomyceteae Fasci. 4 (in preparation).

Specimens examined: from above-mentioned range of distribution.

SEPULTARIA (Cooke) Boud.

* S. *arenicola* (Lév.) Massee, half buried in soil, mid-August to mid-September, Tehri Road, Mussoorie, uncommon. PUI; BPI; CUP-I 33 = LRB 109.

S. *arenosa* (Fuckel) Boud., half buried in soil, The Park, Mussoorie, September, uncommon, (*60*: 199). PUI-136; BPI; CUP-I 34 = LRB 112.

THECOTHEUS Boud.

* *T. pelletieri* (Crouan) Boud., on cow dung, Jabber Khet and other localities around Mussoorie, July to September, uncommon, (*6*: 70). PUI; CUP-I 35, 189 = LRB 157 and 897, respectively.

TRICHARIA Boud.

T. gilva (Boud.) Boud., on soil, Dalhousie, September, uncommon, (material not examined in fresh condition), (*52*: 197). PUI; DU.

TRICHOPHAEA Boud.

* *T. albospadicea* (Grév.) Boud., on soil, Kempty Falls and the Park, Mussoorie, August to September, uncommon, (*6*: 80, 87-90). PUI; CUP-I 36.

T. brunnea (Alb. & Schw. *ex* Fr.) Batra, on burnt ground, Jabber Khet and other localities around Mussoorie, July to September, common, (*6*: 15; *60*: 196). PUI-133 = BPI; PUI-134; CUP-I 37, and 198 = LRB 113 and 912, respectively.

T. gregaria (Rehm) Boud., on soil, The Park, Mussoorie, August to September, uncommon, (*61*: 26). CUP-I 62 = LRB 180.

T. himalayensis Batra, Mycologia 52: 524, on soil, September, (*6*: 12; *63*: 831). PUI-161; BPI; CUP-I 38. *Synonym Sphaerospora tuberculata* Thind, Cash and Sethi, Mycologia *49*: 831.

T. mussooriensis (Thind, Cash & Sethi) Batra, Mycologia 52: 524, on soil, Dhanolti near Mussoorie, (*63*: 834). PUI-163 (Type); BPI.

Family HELVELLACEAE

GYROMITRA Fr. *non sensu* Boud.

G. infula Schaeff. *ex* Fr. pileus saddle-shaped throughout, dark brown (or reddish-brown when young); stipe fluted, white; on soil, Tehri Road and other localities around Mussoorie, July to August, common, PUI; CUP-I 44. (Fig. 21-23.)

HELVELLA L. *ex* Fr.

A study of tissue structure of the forms included in *Leptopodia* Boud., species of *Acetabula* Fuckel (*Paxina* Kuntze *sensu* Seaver), and *Macropodia* Fuckel indicates that all these forms are very closely related and can be referred to the genus *Helvella*. Superficially, some species of *Paxina sensu* Seaver at some stages of development can be referred to either *Helvella* or even stalked *Pustularia*. Thus, the present author has treated these forms under the genus *Helvella*, (Batra, 1963).

H. acetabulum (L. *ex* Fr.) Quél., on soil under coniferous woods, Lal Tibba and other localities around Mussoorie and Dalhousie, (*5*: 98; *52*: 55). PUI-128; BPI; CUP-I 39 = LRB 97; CUP-I 101 to 103 = LRB 857, 894, and 1032, respectively. (Figs. 24-28, 34, 36, 94.)

* *H. atra* König *ex* Fr. on soil, throughout North Western Himalayas, July through September, CUP-I 74 = LRB 1035; LRB 1034. (Figs. 29-33, 35, 37, 95.)

* *H. calyciformis* Batt. *ex* Quél., on soil, widely distributed throughout North Western Himalayas. (*54*: 30). PUI-147, 148; BPI; CUP-I 45, 106, 107, and 186 = LRB 188, 861, 1033 and 1124, respectively. (Figs. 38, 41-46, 50, 96.)

H. crispa (Scop.) Fr., soil, all over the North Western Himalayas, (from Naini Tal to Siri Nagar, Kashmir), (July) August to September, common, (*20*: 11; *26*: 13; *51*: 18; *43*: 374). PUI; BPI; CUP-I 41, 97, 98 = LRB 190, 1122 and 1123. (Figs. 39, 40, 47, 97.)

H. elastica Bull., *ex* Fr. on soil, under coniferous woods, The Park, Mussoorie, Dalhousie, and Siri Nagar (Kashmir), August to September, uncommon, (54: 338). PUI; CUP-I 42, 100 = LRB 187 and 952, respectively. (Figs. 48, 51 to 77, 98.)

* *H. ephippium* Lév., on soil, The Park, Mussoorie, August to September, PUI, CUP-I 82 to 95 = LRB 1071, 860, 944, 951, 965, 1036 to 1038, 1070, 1072, 1073, 1118 to 1120, respectively. (Figs. 49, 78 to 85.)

* *H. lactea* Boudier (Batra, 1963) on soil, The Park, Mussoorie, September, rare, CUP-I 40 = LRB 133 (Fig. 86).

* *H. lacunosa* Afzelius *ex* Fr., on soil, common, Lal Tibba, Mussoorie, August-September, CUP-I 78 = LRB 156. (Figs. 87 to 92, 99.)

* *H. sulcata* Afzelius *ex* Fr. *var. typica*, on soil, Jabber Khet, Mussoorie, CUP-I 76, 79, and 81 = LRB 1125, 893 and 1117, respectively. (Fig. 93.)

* *H. sulcata* Afzelius *ex* Fr. *var. cinerea* Bresdola, on soil, throughout Mussoorie Hills, PUI; CUP-I 77 = LRB 155 and CUP-I 80 = LRB 985.

MORCHELLA Dill. *ex* Fr.

* *M. angusticeps* Peck., on soil, Siri Nagar (Kashmir), September, (only one collection known to the author and it is suspected that this species may grow in abundance early in monsoons). CUP-I 46 = LRB 199. (Fig. 100.)

M. esculenta L. *ex* Fr. Pers., pileus very variable in shape and size, tan to almost dark brown, or soil, distributed throughout North

Western Himalayas, abundant in Kashmir, (*20*: 12; *22*: 44; *24*: 181, 441; *25*: 16; *36*: 338; *51*: 8-10; *57*: 374; *58*: 158). PUI; BPI; HCIO; DD; LAH; K; CUP-I 47 = LRB 200; NY. (Figs. 101, 102.)

The author has examined the material of *M. conica* Pers. *sensu* Seaver, *M. crassipes* (Vent.) Pers. *sensu* Seaver, and *M. deliciosa* Fries *sensu* Seaver from India as well as from the U. S. A. There is no difference in the tissue structure of these fungi. When a large collection is available from a single locality and various stages of development can be traced, specimens representing each of these "species" can be found. (Fig. 101.)

OTIDEA Fuckel.

O. leporina Batsch *ex* S. F. Gray, on soil, Lal Tibba, Mussoorie; Dalhousie and Siri Nagar (Kashmir), August to September, common, (*6*: 94, 95; *59*: 53). PUI-127; BPI; CUP-I 48 = LRB 194.

O. Smithii Kanouse, on soil, August and September, Jabber Khet, Mussoorie, (*61*: 225) PUI-300, 301.

PTYCHOVERPA Boud.

P. bohemica (Krombh.) Boud. = *Verpa bohemica* (Krombh.) Schröt = *Morchella gigaspora* Cooke, on soil, Kashmir (*20*: 12; *22*: 442; *24*: 187; *25*: 16; *51*: 14); K. (Fig. 103.)

PUSTULARIA Fuckel *emend.* Boud. (*nonemend.* Rehm).

* *P. bronca* (Peck) Kanouse, on soil, Dhobi Ghat, Mussoorie, August to mid-September, uncommon, (*6*: 104, 105). PUI = BPI.

P. catinus (Holmskj. *ex* Fr.) Fuckel, on soil, Dhobi Ghat, Mussoorie, September, uncommon, (*6*: 105; *61*: 32). PUI-150, 151; BPI; CUP-I 49 = LRB 105.

VERPA Swartz *ex* Persoon.

* *V. conica* Swartz *ex* Pers., on soil, Darjeeling, September, rare. (Fig. 104.)

INOPERCULATE DISCOMYCETES

Family SCLEROTINIACEAE

BOTRYOTINIA Whetzel.

B. ricini (Godfrey) Whetzel, on inflorescence and fruits of *Ricinus communis*, Mysore, (*20*: 13; *34*: 82). HCIO.

RUTSTROEMIA Karsten.

* *R. macrospora* (Peck) Kanouse *in* Wehm., apothecia 5-12 mm, hymenium dirty white, on rotten wood, The Park, Mussoorie, August, uncommon. PUI; CUP-I 50.

* *R. petiolorum* (Roberge) White, apothecia 1-2 mm, hymenium ochraceous to pale brown, on mid-ribs and petioles of fallen leaves

(usually of *Quercus incana*), widely distributed around Mussoorie, July to September, abundant. PUI; CUP-I 51 = LRB 159.

* *R. longipes* (Cooke & Peck) White, apothecia 1-5 mm in diameter, hymenium mustard yellow, becoming brownish on drying, on petioles of *Fraxinus* spp., Jabber Khet, Mussoorie, September, uncommon. PUI.

* *R. prumi-serotinae* Whetzel & White, on *Prunus* leaves, Municipal Park, Mussoorie, September. CUP-I 199 = LRB 889.

CHLOROCIBORIA Seaver *ex* Korf *et al.*

* *C. rugipes* (Peck) Ramamurthi & Korf, apothecia 2-5 mm, hymenium olive green, on rotten wood, Lal Tibba, Mussoorie, August to September, common in this locality. PUI.

C. aeruginosa (Oed. *ex* Gray) Seaver, apothecia 1-3 mm, hymenium aeruginous green, on rotten wood, Jabber Khet, Mussoorie, September, uncommon, (*17*: 210; *20*: 10; *43*: 153; *51*: 318). PUI; K.

MONILINIA Honey.

M. fructicola (Winter) Honey, apothecia 1-1.5 cm, hymenium pale brown, on fruits of *Prunus* spp., Siri Nagar (Kashmir), September, common. The organism was also reported attacking *P. persica* by Butler & Bisby (1931). (*20*: 13; *34*: 82). HCIO.

SCLEROTINIA Fuckel.

S. sclerotiorum (Lib) de Bary, apothecia 1-1.5 cm, hymenium light brown, widely distributed in the Himalayas, Panjab Plains and other cooler parts of the country, parasitic on several angiosperms, (*10*: 112; *11*: 317; *12*: 39; *13*: 29; *14*: 37; *15*: 40; *20*: 14; *37*: 43; *47*: 126; *67*: 379). PUI.

Family DERMATEACEAE

MOLLISIA Karst.

* *M. cinerea* (Batsch) Karst., apothecia 1-2 mm, hymenium grayish, widely distributed throughout North Western Himalayas, on rotten angiospermous wood, July to September, abundant. PUI.

PSEUDOPEZIZA Fuckel.

P. medicaginis (Lib.) Sacc., on *Medicago sativa*, Kashmir, (*20*: 13). HCIO.

P. repanda (Fr.) Karst., on leaves of *Galium kasauli*, Panjab, (*20*: 13). Butler-1343; HCIO.

P. trifolii (Biv-Bern) Fuckel, on leaves of *Trifolium* sp., Pathankote, "Kashmir," (*20*: 13). PUI; HCIO.

Family HYALOSCYPHACEAE

DASYSCYPHUS S. F. Gray.

D. aleurodes Cooke, on small twigs, Mussoorie, August to September, (*20*: 10; *30*: 73). PUI.

* *D. aspidicola* Sacc. on *Aspidium* frond, Jabber Khet, Mussoorie, July, CUP-I 180 = LRB 915.

D. clandestinus (Bull. *ex* Fr.) Fuckel, on rotting wood, Jabber Khet, Mussoorie, August, (*16*: 204; *20*: 10). PUI.

* *D. crucifera* (Phil.) Sacc., on dead wood, Cemetery, Camel's Back Road, Mussoorie, July and August, CUP-I 179 = LRB 1178.

DASYSCYPHELLA Tranz.

D. cilaris (Schrad.) Sacc., on leaves of *Quercus* sp., uncommon, Mussoorie, August and September. CUP-I 200 = LRB 890.

D. indica Cash, on mossy bark of trees, Mussoorie, (*31*: 724). BPI.

Family GEOGLOSSACEAE

GEOGLOSSUM Pers. *ex* Fr.

G. alveolatum (Rehm) Durand, ascophores 2-4 cm high, hymenium black, on soil, Kempty Falls, Mussoorie, Simla, and Dalhousie, September, common, (*20*: 11). CUP-I 52.

* *G. cohaerens* Durand, ascophores 1.5-2.5 cm high, on soil, Mussoorie, September, CUP-I 142 = LRB 1094. (Figs. 105, 106.)

* *G.* (?) *fallax* Durand, on soil, September, CUP-I 145 = LRB 1059. (Fig. 107.)

G. glabrum Pers. *ex* Fr. = *G. ophioglossoides* (W.) Sacc., ascophores 1.2 cm high, hymenium black, on soil, Kempty Falls, Mussoorie, Dalhousie, and Yeumtong, September, uncommon, (*17*: 209; *20*: 11; *24*: 7; 39: 21; *51*: 43). PUI; CUP-I 53, 132 and 133 = LRB 104, 1097, 1089, respectively. (Figs. 108-112.)

* *G. japonicum* Imai, ascophores 3-5 cm high, on soil, Mussoorie, September, CUP-I 129 = LRB 1095. (Figs. 113, 114.)

* *G. nigritum* (Fr.) Cooke, on soil, Mussoorie, September, CUP-I 134 to 141 = LRB 1108, 1104, 1093, 1092, 1056, 1052A, 1051, and 1050, respectively. (Figs. 115-118.)

* *G. pygmeum* Gerard, ascophores 1-2.5 cm high, on soil, Mussoorie, September. CUP-I 130, 131 = LRB 1087, 1058, respectively. (Figs. 119, 120.)

* *G. simile* Peck, ascophores up to 2.5 cm high, dark brown to black, on soil, Mussoorie, September, CUP-I 185 = LRB 1084. (Figs. 121, 122.)

GLEOGLOSSUM Durand.

* *G. glutinosum* (Pers. *ex* Fr.) Durand, ascophores 5-8 cm high, hymenium brownish-black, on soil among mosses, Dalhousie, September, common. PUI; CUP-I 54, 126, and 127 = LRB 186, 1063, 1052, respectively. (Figs. 123-128.)

LEOTIA Pers.

* *L. chlorocephala* Schw., stipe with bluish color, on soil, Mussoorie, August. CUP-I 150 = LRB 1113.

* *L. lubrica* Scop. *ex* Fr., ascophores 4-8 cm high, hymenium greenish or olive, on soil, widely distributed throughout North Western Himalayas, Sikkim, July to September, (*16*: 202; *20*: 11; *24*: 97). PUI; CUP-I 55, CUP-I 147 to 149 = LRB 1116, 1115, 1114 respectively. (Figs. 129-132.)

* *L. stipitata* (Bosc.) Schröter, ascophores 3-7 cm high, hymenium aeruginous green, on soil, Jabber Khet and Balharu Khud, Mussoorie, August to September, uncommon. PUI; CUP-I 56 = LRB 198.

MICROGLOSSUM Gill.

* *M. olivaceum* (Pers. *ex* Fr.) Gill. on soil, ascophores 5-7 mm high, tan color, Chakrata Road, Mussoorie, CUP-I 114 = LRB 999.

M. viride (Pers.) Gill. ascophores 3-5 cm high, hymenium greenish-yellow, on soil, Dalhousie, September. (*17*: 209; *24*: 9; *51*: 38). PUI.

MITRULA Fr. *emend.* Imai (*sensu stricto*, type species *M. paludosa* Fr.).

Mitrula sp. (Description based on collection CUP-I 113 = LRB 1110.) (Figs. 133, 134.)

Ascomata gregarious, tan color, 3 cm tall; *ascigerous* portion 1.6 cm x 1-2 mm, compressed or flattened, tan, becoming dark brown on drying, with a distinct median groove, stipe terete (finger-like) 1-1.5 cm x 0.5-1 mm; *hymenium* spread all over the ascigerous portion, 90 μ thick, pale yellow; *subhymenium* distinct from medulla, compact and of textura intricata, cells narrower than that of medulla; *medulla* pale yellowish, of textura porrecta, cells large, freely anastomosing, septate and do not easily stain with lactophenol-cotton blue; *asci* cylindrical, gradually tapering towards the base, 8-spored, do not stain blue with iodine solution, and arising from croziers, 83-105 x 6-6.5(7.5) μ; *ascospores* uniseriate, or partially biseriate near the apex, almost filling the entire ascus, hyaline, narrowly ellipsoid, non-septate, transversely striated, the striations

consisting of bands of cytoplasm, the number of bands varying from one to three or rarely five (these bands stain with Phloxine, Cotton Blue and can be easily confused with septa), 11-13 x 4-5 μ; paraphyses branched or unbranched, quite often bifurcate near the apex, closely septate near the base, subhyaline to pale yellowish in thick sections, 2-3 μ broad, 4-5 μ above. On soil, collected from Chakrata Road, Mussoorie, September 12, 1960.

The ascospores of this *Mitrula* sp. are quite characteristic and distinct from hyaline-spored members of the family *Geoglossaceae* reported in the literature. Occasionally the spores bud out small microconidia which are often placed near the ends. The spores remain unseptate throughout and reminds one of some similar cases in the genus *Leotia*. There is no trace of mucilage present in ascomata of this fungus and therefore, it does not belong to the genus *Leotia*.

TRICHOGLOSSUM Boud.

T. hirsutum (Pers. *ex* Fr.) Boud., ascophores 4-9 cm high, hymenium black, on soil, common throughout Himalayas, September. (*20*: 11; *39*: 12). PUI; CUP-I 57; CUP-I 107 to 112 = LRB 1101, 1099, 1098, 1088, 1085, 1060. (Figs. 139-142.)

* *T. wrightii* Durand, ascophores 2-3 cm high, hymenium black, on soil, Mussoorie, August to September, common. PUI.

* *T. octopartitum* Mains, ascophores 2-3.5 cm high, black, on soil, throughout Mussoorie Hills, September, CUP-I 123 to 125 = LRB 1096, 1062, and 1105, respectively. (Figs 135-138.)

Family HELOTIACEAE

HELOTIUM Fries

H. citrinum Hedw. *ex* Fr., on rotten twigs and plant debris, widely distributed in North Western Himalayas, (*16*: 205; *20*: 11; *31*: 128). PUI.

Family ORBILIACEAE

Many species of both the genera of this family, the genus *Orbilia* Fries and the genus *Hyalinia* Boudier are known from India. No authentic material for comparison was available at this stage and thus the specific names have not been determined. The apothecial margin in *Orbilia* is even and the paraphyses are abruptly swollen while the apothecial margin is dentate and paraphyses without abrupt swellings in *Hyalinia*.

PART II

DISCOMYCETE TAXA NOT EXAMINED

Material pertaining to the following taxa has not been examined by the authors:

Aleurina orientalis (Pat.) Sacc. and Sydow *in* Sydow and Butler (1911), on cow dung, Pusa, (*20*: 10; *57*: 374).

Ascobolus gollani P. Henn., "on manured ground under trees, Botanic Garden, Saharanpur," (*20*: 10; *36*: 338).

A. indicus Sanwal, on cow dung, Delhi, (*53*: 202). DU.

Boudiera seaveri Sanwal, on soil, Kalka (Kumaon Hills), June, (*52*: 194).

Bulgaria inquinans Fr. *var. chalybea* Berk., on wood, Darjeeling, (*16*: 205; *20*: 10; *28*: 74).

Dasyscyphus emerici (Berk. & Phill.) Sacc., on twigs, Nilgiris, (*20*: 11; *28*: 74).

Erinella corticola Massee, on bark, Dehra Dun, (*20*: 11; *21*: 727; *42*: 115).

Discomycetella aquatica Sanwal, on rotten wood, Lachman Jhoola, Hardwar, (*53*: 200). DU.

Geoglossum (?) *alveolatum* Durand, on ground, Simla, (*20*: 11).

Helvella fargessii Pat., (*20*: 11; *39*: 5).

Helotium malloti Ramakrishnan & Srinivasan, (*50*: 157).

Helotium pusense Sydow, on *Ricinus communis*, (*20*: 11; *57*: 374).

H. quercifolium Thind, Cash & Singh "on dead leaves of *Quercus incana* Roxb." (*66*: 836).

Humaria glareosa (Velenovsky) Thind & Sethi, on soil, The Park, Mussoorie, (*61*: 26). PUI-144 = BPI.

H. gregaria Rehm., on soil, Kadukhal near Mussoorie, (*16*: 26). PUI-143 = BPI.

H. masseana Sacc. and D. Sacc., Garwahl, (*20*: 11; *43*: 152; *51*: 26).

Humarina indica Thind, Cash and Singh, Mussoorie (*65*: 463). PUI-309 = BPI.

Lachnea geneospora (Berk.) Sacc. = *Peziza geneospora* Berk., on rotten wood, Sinchul, (Sikkim), (*16*: 203; *20*: 11; *24*: 72; *51*: 178).

Lachnella nilgherrensis Cooke, on herbaceous stems, (*20*: 11; *28*: 73).

Lamprospora trachycarpa (Curr.) Seaver *var. ferruginea* (Fuckel) Thind and Sethi, on soil, Dhanolti near Mussoorie, (*60*: 199). PUI-135A = BPI.

Midotis indica Thind, Cash & Sing., "on dead and decaying stems of oak," (*66*: 833).

Mitrula rosea Lloyd, on earth, (*20*: 12; *40*: 885).

Mitrula agharkarii Banerji, on soil, Senchal Range, Darjeeling, (*5*: 308).

Neotiella catharinea Mclennan & Halsey, in the axils of leaves of the moss *Catharinea mulleri*, Darjeeling. From the description it appears to be synonym of *Aleuria rutilans* (Fr.) Gillet.

Ombrophila indica Sydow, on rotten wood, Dehra Dun, (*20*: 12; *57*: 375).

Otidea darjeelensis (Berk.) Sacc., on ground, Darjeeling, (*16*: 202; *20*: 12; *23*: 30; *24*: 125).

Patella ricciophila Seaver, associated with *Riccia* spp., Naini Tal, November, (*52*: 23). DU.

Perrotia fusca E. Müller & Dennis, on dead branches of *Lonicera Quinquelocularis* "Himalaya," India, (*44*: 46).

P. himalayensis E. Müller & Dennis, on dead branches of *Lonicera purpurascens* "Himalaya" India. (*44*: 48.)

P. lonicerae (Alb. & Schw. *ex* Fr.) E. Müller & Dennis ? Himalayas, India. (*44*: 44.)

Peziza cerina Pers., on twigs, Bombay (*32*: 309; *35*: 244).

P. epispartica Berk. and Broome, on rotten wood, from "Belgaum," (*19*: 102; *20*: 12; *26*: 96; *51*: 89).

Phialea fructigena (Bull.) Gill., "on stems of dead Umbelliferae," Sikkim, (*16*: 204; *20*: 12).

Plicaria repanda (Wahl.) Rehm, on rotten fruits of *Borassus flabellifer*, Calcutta, (*4*: 35, 36; *20*: 13).

Pseudopeziza skimmiae Padwick, on leaves of *Skimmia laureola* Sieb. & Zucc., Kashmir, (*49*: 1). HCIO.

Pseudoplectania kumaonensis Sanwal, on dead and rotting *Quercus* wood, Lohaghat (Kumaon), (*52*: 191). DU.

Rhizina reticulata Berk. & Broome, on wood, Nilgiris Hills, (*19*: 102; *20*: 13; *51*: 58).

R. zonata Berk., among leaves of *Pinus* spp., Darjeeling, (*17*: 209; *20*: 13; *51*: 59).

Rutstroemia sepiacea Thind, Cash & Singh "on fallen petioles in oak forest" (*66*: 839).

Sarcoscypha macropus (Pers.) Lamb, (*20*: 13).

Sarcoscypha sp., (*56*: 158).

Sarcosoma orientale Patouillard, (see *Aleurina* above).

Tryblidaria lonicerae E. Müller, on *Lonicera* sp. (Sydowia 11, p. 460, original paper not consulted.)

Vibrissea stilboidea (Berk.) Sacc., "on the main nerves of leaves of *Pyrus*," Tonglo, Sikkim, (*16*: 204, 205; *20*: 14; *51*: 53).

V. turbinella (Berk.) Sacc., on leaves of *Pyrus*, Tonglo, Sikkim, (*16*: 204; *20*: 14; *51*: 52).

Misidentifications:

Humaria pygmea (Clements) Thind & Sethi, on soil, Mussoorie, August to September, (*6*: 90, 91; *61*: 29). PUI-145, 146; BPI.

H. glariosa (Vel.) Thind & Sethi. (*61*: 27.) PUI-144, BPI.

Humarina gerardi (Cooke) Seaver var. *gigantea* Thind & Singh (64: 230). PUI 305.

PART III

A KEY TO OPERCULATE INDIAN DISCOMYCETES

1. Apoth. hairy, sessile, actinomorphic (radially symmetrical); (i) hairs well developed, bristle-like, usually conspicuous and sharp-pointed, or (ii) hairs flexuous and tomentose, or (iii) hairs poorly developed, inconspicuous and adpressed to the apoth. ..... 23.
1. Apoth. not hairy, sessile or stipitate, actinomorphic or zygomorphic, 2.
2. Apoth. sessile, apoth. disc cupulate to discoid or scutellate, actinomorphic ..... 9.
2. Apoth. stipitate, or when sessile, then cleft on one side; apoth. disc or pileus usually zygomorphic except in the genera *Pustularia* and *Cookeina* ..... 3.
3. Apoth. usually in thick clusters, apoth. disc cleft and thus appearing spoon-shaped ..... 4.
3. Apoth. not as above ..... 5.
4. Apoth. clusters not subterranean, stroma absent; ascosp. non-striated. Apoth. light brown; ect. excipl. of text. glob. to text. angul.; med. excipl. of loose text. intric.; ascosp. 2-guttulate, ellipsoid, 10-13 x 5-7 μ ..... *OTIDEA leporina.*
4. Apoth. arising in clusters from fleshy, tuberous, subterranean stroma; ascosp. striated ..... *WYNNEA.*

WYNNEA

a. Apoth. dark brown; ascosp. somewhat allantoid, 1-3-guttulate, 30-36 x 14-16 μ ..... *W. americana.*

a. Apoth. light brown; ascosp. ellipsoid, 2-guttulate, 25-30 x 12-14 μ ..... *W. macrotis.*

5. Apoth. disc deep cupulate; lignicolous or terricolous ..... 6.
5. Apoth. disc morchelloid or helvelloid, or if shallow cupulate, then with a large, corrugated stipe; exclusively terricolous ..... 7.
6. Apoth. disc bright colored, exterior covered with fasciculate hairs; asci abruptly attenuated near the base, operculum eccentric; ascosp. striated (in the species dealt with in this key) ..... *COOKEINA.*

6. Apoth. disc dull yellow to light brown, exterior pustulate or warty; asci gradually attenuated near the base, operculum apical; ascosp. non-striated ..... *PUSTULARIA.*

COOKEINA

a. Hym. orange-red or pink.
Ect. excipl. of text. glob.; med. excipl. thin and of text. intric.; hypothecium thick, of text. porr.; ascosp. (24-)28-30 x 12-16 μ, *C. sulcipes.*

a. Hym. pale yellow.
Ect. and med. excipl. indistinguishable, both of text. glob.; hypothecium of text. porr.; ascosp. (28-)30-40 x 10-14 μ, *C. venezuelae.*

PUSTULARIA

a. Apoth. conspicuously warted; ascosp. narrowly ellipsoid, 24-25 x 10-11 μ ..... *P. bronca.*

a. Apoth. minutely verrucose; ascosp. broadly ellipsoid, 14-21 x 10.5-14 μ ..... *P. catinus.*

7. Asci typically 2-spored; pileus campanulate.
Pileus 1-2 cm in diam., up to 3 cm high; stipe 4-6 x 1 cm; ascosp. narrowly ellipsoid, 60-80 x 16-18 μ *PTYCHOVERPA bohemica.*

7. Asci 8-spored; pileus gyrose, cupulate, or saddle-shaped ..... 8.

8. Pileus divided by sterile ridges (costae) into small hymenial areolae; apoth. stipe hollow ..... *MORCHELLA.*

8. Pileus cupulate, remaining so on maturity or becoming saddle-shaped, hym. continuous; apoth. stipe hollow or solid; ascosp. smooth walled, with single large oil globule which in most cases almost fills the ascosp. ..... *HELVELLA.*

MORCHELLA

a. Pileus narrowly conic, light brown, sterile ridges darker than fertile pits; ascosp. 20-26(-29) x 13-15 μ ..... *M. angusticeps.*

a. Pileus broadly conic, yellowish-brown, sterile ridges nearly white to cream-colored; ascosp. (16-)18-22(-26) x 9-12(14) μ, *M. esculenta.*

HELVELLA

a. Stipe strongly corrugated, corrugations reaching at least up to the base of the apoth. disc; stipe more or less concolorous with the ectal surface of the disc, or rarely lighter in shade ..... b.

a. Stipe smooth, rarely a few lacunae present near the base; stipe dark or milk white ..... g.

b. Hym. dark colored, light brown to dark brown; pileus saddle-shaped or cupulate to discoid ..... c.

b. Hym. light colored, cream colored or light brownish yellow; pileus saddle shaped or somewhat irregular in outline, margin of the pileus decurrent and fused with the stipe ..... e.

c. Pileus cupulate to discoid, sometimes becoming curved and deflexed ..... d.

c. Pileus saddle-shaped.
Pileus 1-2.5 cm broad, 1-1.5 cm high, margin decurrent and fused with the stipe; stipe 2-4 cm x 4-10 mm; ect. and med.

excipl. not clearly distinguishable, of text. intric. except for a few globose cells scattered in the outer few layers, together 196-235 μ thick, hyphae 2-4 μ broad; hym. dark brown, 246-278 μ thick; ascosp. 12-16 x 10-12 μ ..... *H. lacunosa,*

d. Hym. and outer surface of apoth. disc greyish- to smoky-brown. Apoth. disc 3-8 cm in diam., 1-3 cm deep; stipe corrugations extending up to the pileus margin; ect. excipl. of text. glob., 246-300 μ thick, cells subhyaline, 10-25 x 10-14 μ; med. excipl. of text. intric., 380-425 μ thick, hyphae 4-5 μ broad, hyaline; hym. light brown, 380-415 μ thick; ascosp. (16-)20-22 x 14-16 μ ..... *H. acetabulum.*

d. Hym. and outer surface of apoth. disk dark brown, 1-3 cm in diam., 0.5-1 cm deep.

Stipe yellowish-brown, stipe corrugations extending only up to the base of the pileus, stipe 3-6 cm x 5-8 mm; ect. excipl. dark brown, of text, glob., 65-130(200) μ thick, outer excipl. cells 20-25 x 10-14 μ, the inner half (60-80 μ) of ect. excipl. approaching text. porr.; med. excipl. of compact text. intric. cells hyaline, hyphae 3-4 μ broad; hym. dark brown, 360-380 μ thick; ascosp. 18-20 x 9-13 μ ..... *H. calyciformis.*

e. Ect. and med. excipl. clearly distinguishable ..... f.

e. Ect. and med. excipl. not clearly distinguishable, of text. intric., 360-400 μ thick, hyphae 2-3 μ broad, at intervals the tips of the hyphae swollen, the outermost layer of the text. intric. thus appearing to be of globose cells 12-19 μ in diam.

Pileus 1-4 cm broad, 2.5 cm high, irregularly saddle-shaped, becoming cerebriform with age, light brownish-yellow, decurrent, fused with and almost totally covering the stipe; stipe 1-3 x 0.8-1.2 cm, white or cream colored, usually narrowed towards the base; hym. 278-312 μ thick; ascosp. 18-20 x 14-15 μ; para. not enlarged above ..... *H. lactea.*

f. Pileus irregularly saddle-shaped, 3-7 cm broad, 1-2 cm high, pale orange-yellow or cream colored.

Stipe 6-11 x 2-2.5 cm, gradually tapering towards the pileus; ect. excipl. of text. glob., 114-160 μ thick, excipl. cells cylindrical, loosely held together to form a fasciculate, hyaline tomentum measuring 36-50 x 10-16 μ; med. excipl. of text. intric., 492-524 μ thick, hyphal cells 3-4 μ broad; hym. 400-425 μ thick; ascosp. 16-22 x 9-12 μ; para. slightly enlarged above ..... *H. crispa.*

f. Pileus saddle-shaped, 1.5-2 cm broad, 1 cm high, light brownish-yellow.

Stipe 4-5 cm x 5-8 mm, of uniform thickness throughout; ect. excipl. of text. glob., 50-80 μ thick, cells columnar, 28-36 x 7-14 μ; med. excipl. of text. intric., 450-500 μ thick, hyphae 3-4 μ broad; hym. 328-380 μ thick; ascosp. 12-18 x 9-11 μ; para. not enlarged above ..... *H. sulcata.*

g. Pileus typically saddle-shaped ..... h.

g. Pileus cupulate to discoid, sometimes the margin recurving upward and inward, brown to dark brown.

Pileus 1-1.8 cm in diam., up to 1 cm deep; stipe 4-6 cm x 2-4 mm, dark brown to black; ect. excipl. of text. glob., 100-200 μ thick, the individual cells drum-shaped (broadest in the middle), light brown, forming a fasciculate tomentum; med. excipl. of text. intric.; hym 320-350 μ thick; ascosp. 17-20 x 8-10 μ; para. slightly enlarged above, *H. ephippium*.

h. Pileus cream to tan colored, stipe milk white.

Pileus 1-2 cm broad, 1.5 cm high; stipe white, 4-8(-10) cm x 3-5 mm; ect. excipl. of text. angul., 144-180 μ thick, individual cells 18-29 x 14-18 μ; med. excipl. of text. intric., 126-144 μ thick, hyphae 3-4 μ broad; hym. 300-328 μ thick; ascosp. 18-22 x 11-15 μ ..... *H. elastica*.

h. Pileus dark brown to black, stipe brown to dark brown with occasional white patches near the base.

Pileus 1-2 cm broad, 0.5-1 cm high; stipe tapering towards the pileus, 3-5 cm x 2-3 mm; ect. excipl. of text. prismatica, 60-80 μ thick, cells club shaped and elongated outward, dark brown, 15-38 x 7-11 μ, med. excipl. of text. intricata, light brown, 150-200 μ thick, hyphae 4-5 μ; hymenium brown to dark brown, 225-255 μ thick; ascospores 15-19 (-22) x 11-12 μ ..... *H. atra*.

9. Ascosp. violet, later becoming brown, usually surrounded by a mucilaginous sheath; asci protruding above the hym. in fresh material; fimicolous (except *Ascobolus carbonaria* and *A. geophilus*) ..... 10.

9. Ascosp. hyaline, rarely light brown; asci sometimes protruding above the hym.; humicolous, terricolous, on charcoal beds, fimicolous or lignicolous ..... 11.

10. Ascosp. in a common mucilaginous sheath forming an ellipsoid ball measuring 40-60 x 20-24 μ.

Individual ascosp. broadly ellipsoid, brown, walls minutely tuberculate, 23-27 x 9-10 μ; asci broadly clavate or sub-globose, 120-130 x 26-30 μ, apoth. up to 1 mm in diam., golden yellow; on horse or cow dung ..... *SACCOBOLUS kerverni*.

10. Ascosp. free from one another ..... *ASCOBOLUS*.

ASCOBOLUS

a. Apoth. on soil, 1-2 mm in diam., reddish brown, ascosp. with reticulations, 26-30 x 11-13 μ ..... *A. geophilus*

a. Apoth. on dung ..... b.

b. Mature apoth. discs small, 1-5 mm in diam. ..... c.

b. Mature apoth. discs large, 5 mm-2.5(-3) cm in diam.

Apoth. disc externally pale to golden yellow; hym. concolorous with exterior; asci slightly curved near the tips, 150-215 x 19-21 μ; ascosp. minutely verrucose when mature, 22-24 x 11-12 μ; para. 3-4 μ broad, up to 6 μ above; on cow and buffalo dung ..... *A. magnificus*.

c. Ascosp. less than 30 μ long, 16 μ broad, distinctly sculptured, sculpturing consisting of either reticulations or warts ..... d.

c. Ascosp. (40-)50-60 x (27-)30 μ, walls sculptured, sculpturing consisting of reticulations (not all the ascosp. show reticulations clearly).
Ascosp. arranged irregularly in the ascus; asci broadly clavate; para. 1-2 μ broad, not enlarged above; apoth. disc 1-2 mm ..... *A. immersus.*

d. Asci cylindrical with ascosp. in the upper half or completely filling the ascus ..... e.

d. Asci clavate, ascosp. contained in the upper half only.
Ascosp. narrowly ellipsoid, sculpturing reticulate, 20-26 x 10-13 μ; para. 2-4 μ broad, branched near the apex; apoth. up to 5 μ in diam., exterior golden yellow; hym. brown; on cow dung and human excreta ..... *A. stercorarius.*

e. Ascosp. ellipsoid, rarely sub-globose, tuberculate, 17-24 x 14-15 μ. Asci 180-200 x 18-25 μ, with ascosp. in the upper half; para. curved, 2-3 μ broad, slightly enlarged above; apoth. 5-6 mm in diam., exteriorly camel-brown; hym. brown; on burnt ground ..... *A. carbonaria.*

e. Ascosp. narrowly ellipsoid, wall ornamentations reticulate, (19-)26-30 x 14-16 μ.
Asci 92-110 x 26-30 μ, with ascosp. completely filling the asci; para. 2-3 μ, not enlarged above; apoth. 3-4 mm in diam.; on dung ..... *A. taxonomic sp.* V.

11. Ascosp. non-striated; operculum centric; plants of temperate or subtropical climate ..... 12.

11. Ascosp. longitudinally striated; operculum eccentric; plants lignicolous, from warmer climates or lower altitudes.
Apoth. disc up to 5-7 cm in diam., attached to the wood by a broad base; hymenium purplish-red to reddish-brown; ect. excipl. of compact text. intric.; med. excipl. of loose text. intric.; ascosp. unequal-sided (somewhat allantoid), 24-30 x 9-13 μ,
PHILLIPSIA domingensis.

12. Asci with a distinctly thickened ring of callose-pectose near the apex. Apoth. 1-2 mm in diam.; hym. orange-red to scarlet red; ect. excipl. of text. porr.; med. excipl. of text. intric.; ascosp. 2-guttulate, smooth-walled, 12-18 x 7-9 μ,
PSEUDOPITHYELLA miniscula.

12. Asci not as above ..... 13.

13. Mature ascosp. globose ..... 14.

13. Mature ascosp. ellipsoid or fusoid ..... 18.

14. Asci not turning blue in iodine, apoth. exteriorly smooth ..... 15.

14. Asci turning blue in iodine, apoth. exteriorly warted ..... *PLICARIA.*

PLICARIA

a. Ect. excipl. of text. prism.; med. excipl. either not distinguishable from the ect. excipl. or of text. intric.; ascosp. verrucose or tuberculate; para. conspicuously enlarged above ..... b.

a. Ect. excipl. of text. glob.; med. excipl. of text. intric.; ascosp. strongly spinulose; para. not enlarged above.

Apoth. very short-stipitate, externally tuberculate, tubercles pyramidal, 36-54 x 21-36 μ; apoth. disc 1-1.2 cm in diam.; ascosp. 1-guttulate, pale brown, spinulose, 13-18 μ in diam., spines 2-3 μ high, up to 1.5 μ broad at the base,
P. pseudoplanchonis.

b. Ect. and med. excipl. not clearly distinguishable; hym. purple-brown.
Apoth. cupulate, sessile, externally tuberculate, apoth. disc 5-10 mm in diam., exteriorly dark brown, with a crenate margin; ascosp. light brown, 1-guttulate, verrucose, ornamentations of small tubercles, 17-18(-19) μ in diam.,
P. papillosa.

b. Ect. and med. excipl. distinguishable, the latter of text. intric.; hym. light brown.
Apoth. discoid or shallow cupulate, the exterior tubercles pyramidal, 100-200 μ high, 80-246 μ broad; apoth. disc 1-2 cm in diam.; ect. excipl. of text. prism., cells 16-28 x 11-15 μ; med. excipl. 500-700 μ thick, hyphae 7-11 μ broad; hym. 280-325 μ thick; ascosp. 1-guttulate, verrucose, 16-20 μ; para. 3-4 μ broad, up to 8.9 μ above; on burnt places,
P. trachycarpa var trachycarpa.

15. Apoth. substipitate, externally covered with flexuous hyphae; ascosp. smooth; hym. black or yellow to orange-red; on *Cupressus* spurs, or dead sticks of deciduous trees ..... 16.

15. Apoth. sessile, flexuous hyphae absent; ascosp. smooth or sculptured; terricolous ..... 17.

16. Apoth. disc 1-2 mm in diam.; hym. pale- to orange-red.
Ascosp. 8-10 μ in diam., with a single large oil globule almost filling the interior; hair-like flexuous hyphae colorless; on dead spurs of *Cupressus* spp. ..... *PITHYA cupressi.*

16. Apoth. disc 5 mm-2.8 cm; hym. brownish-black.
Ascosp. 12-16 μ, with a large oil drop sometimes surrounded by several smaller ones; hair-like flexuous hyphae dark brown; on dead roots or twigs ..... *PSEUDOPLECTANIA nigrella.*

17. Para. curved or hooked; ect. excipl. of text. angul. or text. porr.; ascosp. smooth ..... *PULVINULA.*

17. Para. not curved or hooked, ect. excipl. of text. glob. or text. prism.; ascosp. smooth or sculptured ..... *LAMPROSPORA.*

PULVINULA

a. Hym. pink or bright red; apoth. discs cupulate to discoid ..... b.

a. Hym. cream colored; apoth. discs discoid.
Ect. excipl. of text. angul., 50-70 μ thick; med. excipl. of compact text. intric., 30-40 μ thick; ascosp. 15-18 μ in diam., with a single large oil globule; on soil ..... *P. discoidea.*

b. Ascosp. with one large and several small oil globules.
Apoth. 2-4 mm in diam.; hym. bright red; ascosp. 10-12 μ in diam.; para. 2-3 μ broad, up to 5 μ above; on eroded soil,
P. constellatio.

b. Ascosp. with several small oil globules completely filling the interior.

Apoth. 1-2 mm; hym. pink when fresh, turning brownish on drying; ascosp. 12-14 μ in diam.; para. not enlarged above; on burnt places overrun by mosses,

P. carbonaria var. *brevispora* L. R. Batra *var. nov.*

[*Ascosporae parviores quam P. carbonaria* (Fuckel) Boudier *var. typica*]

LAMPROSPORA

a. Ascosp. smooth walled; apoth. disc. 2-5 mm ..... b.

a. Ascosp. sculptured; apoth. disc 5 mm - 4 cm except in lead "c" below ..... d.

b. Hym. orange-red, light brown or camel brown; ascosp. with one, two, or many oil globules ..... c.

b. Hym. whitish to cream colored; ascosp. with single, large, central oil globule.

Asci. cylindrical, 220-260 x 10-14 μ, ascosp. 10-14 μ in diam.; para. 3 μ broad, slightly enlarged above,

L. taxonomic sp. VII.

c. Hym. orange-red; ascosp. 12-13 μ in diam., with 5-9 small oil globules ..... *L. multiguttula.*

c. Hym. light brown to brown; ascosp. (11-)14-17 μ in diam., with single large oil globule ..... *L. chopraiana.*

d. Ascosp. strongly spinulose and hyaline or brown; on burnt ground ..... e.

d. Ascosp. minutely verrucose, pale brown; on soil.

Apoth. disc 5-9 mm in diam., externally smooth, purple-brown; ect. excipl. of text. glob., up to 36 μ thick, cells 18-25 x 10-15 μ; med. excipl. of text. intric., 82-114 μ thick, hyphae 3-4 μ broad; hym. 213-246 μ thick; purple-brown pigment from dried material water-soluble; ascosp. 1-guttulate, ornamentations inconspicuous, (9-)11-13 μ in diam.; para. 3-5 broad, branched near the apex, tips slightly enlarged ..... *L. planchonis.*

e. Apoth. disc cupulate, exteriorly light orange, 0.5-1 mm in diam.; hym. orange-yellow to orange-red; ascosp. hyaline.

Ect. excipl. of large text. glob., sometimes giving out hair-like flexuous hyphae; med. excipl. of loose text. intric. approaching text. glob.; asci cylindrical, 240-280 x 24-28 μ; ascosp. with single large oil globule, 20-24 μ in diam.; para. 2-3 μ broad, up to 7-8 μ above ..... *L. spinulosa.*

e. Apoth. disc discoid, exteriorly light brown, 3-4 cm in diam.; hym. brown; ascosp. light brown.

Ect. and med. excipl. together 1-1.5 mm thick; asci cylindrical, 270-290 x 14-16 μ; ascosp. with single large oil globule, 13-15 μ; spines up to 1.5-2.0 μ high, up to 1 μ broad; para. 5-6 μ broad, slightly swollen above. Spines 1.5-2.0 μ,

L. taxonomic sp. IX.

18. Asci 8-spored, not very conspicuous, visible to the naked eye only when ascosp. colored; ascosp. mostly uniseriate, rarely biseriate or irregularly arranged ..... 19.

18. Asci 32-spored, very large and protruding above the grayish hym., visible with the naked eye; ascosp. arranged irregularly in 3-4 rows. Ascosp. 30-40 x 20-21 μ; apoth. 1-2 mm in diam.; plants coprophilous . . . . . *THECOTHEUS pelletieri.*

19. Apoth. not confluent or cespitose; mycelial mat or subiculum absent, 20.

19. Apoth. usually very gregarious and cespitose, on thick mycelial mat or subiculum; on burnt ground or heated places, *PYRONEMA omphaloides.*

20. Ascosp. smooth or variously ornamented, ornamentations never reticulate; apoth. variously colored . . . . . 21.

20. Ascosp. with reticulate ornamentations; apoth. bright orange or scarlet red; para. swollen above . . . . . *ALEURIA.*

ALEURIA

a. Ascosp. apiculate at one or both ends; apoth. disc 2-8 cm in diam.; para. up to 9 μ above; on bare soil . . . . . c.

a. Ascosp. non-apiculate; apoth. disc 2-3 mm to 2 cm in diam.; para. up to 7 μ above . . . . . b.

b. Apoth. 2-3 mm in diam.; on soil among or on mosses; ascosp. 19-26 x 10-13 μ; para. 3-4 μ broad, enlarged above, *A. rutilans.*

b. Apoth. 1-3 cm in diam.; occurring in clusters under coniferous trees, ascosp. 16-20 x 10-12 μ . . . . . *A. rhenana.*

c. Hym. scarlet red; tomentum light brown. Apoth. sessile; ascosp. 24-26 x 10-13 μ . . . . *A. rubra.*

c. Hym. orange; tomentum hyaline. Apoth. sessile or short stipitate; ascosp. 15-18(-20) x 7-9 μ, *A. aurantia.*

21. Apoth. small, less than 10 mm in diam.; asci sometimes turning blue with iodine; coprophilous, terricolous or lignicolous . . . . . 22.

21. Apoth. usually more than 10-12 mm in diam.; asci turning blue with iodine; terricolous . . . . . *PEZIZA.*

PEZIZA

a. Ascosp. smooth walled; apoth. light colored b.

a. Ascosp. ornamented with small warts or spines; apoth. dark colored . . . . . d.

b. Apoth. large, 3-8 cm in diam., deep cupulate or repand, sessile, cream colored to white; hym. light brown or smoky brown . . . . . c.

b. Apoth. 0.5-1.5 cm in diam., shallow cupulate to discoid, short-stipitate or subsessile, bluish-violet; hym. pink-violet. Hym. 225-270 μ thick; ascosp. 28-31 x 8-10 μ, 1-guttulate; para. 3 μ broad, slightly enlarged above; on soil, *P. gerardii.*

c. Apoth. on heavily manured soil, deep cupulate; hym. smoky brown. Hym. 300-350 μ thick; med. excipl. of text. glob., cells 70-100 x 70-90 μ; ect. excipl. of text. intric., hyphae 5-8 μ broad; ascosp. 23-26 x 10-12 μ; para. up to 3-4 μ broad, *P. vesiculosa.*

c. Apoth. on wood, shallow cupulate, becoming repand; hym. light brown.
Ascosp. 14-16 x 8-10 μ; para. not enlarged above, *P. repanda.*

d. Apoth. flesh, ect. and med. excipl. not turning golden yellow when broken ..... e.

d. Apoth. flesh turning golden yellow when broken.
Asci 260-300 x 10-14 μ; ascosp. ornamentations consisting of small warts; ascosp. 16-20 x 8-12 μ; para. 4 μ broad, up to 10 μ above ..... *P. succosa.*

e. Ascosp. ornamentations of conspicuous warts or spines, reticulations absent ..... f.

e. Ascosp. ornamentations consisting of elongated ridges which anastomose to form a reticulum.
Apoth. 2-4 cm in diam., disc-exterior and hym. brown; hym. 328-360 μ thick; ect. excipl. 50-60 μ thick, of text. glob., cells 11-18 x 10-17 μ; med. excipl. 246-278 μ thick, of text. intric., hyphae 2-3 μ broad; ascosp. 2-guttulate, hyaline, 16-18 x 8-9 μ; para. very few, 2-3 μ broad, not enlarged above ..... *P. taxonomic sp.* X.

f. Ascosp. eguttulate; apoth. 3-7 cm in diam., exteriorly pustulate; on burnt ground ..... g.

f. Ascosp. 2-guttulate, rarely 3-guttulate, hyaline; apoth. 1-3 cm in diam.; on soil ..... h.

g. Ascosp. light brown; apoth. exteriorly light brown.
Hym. reddish to dark brown; asci 250-300 x 12-14 μ; ascosp. verrucose, warts up to 1.5 μ high; para. 2-3 μ broad, up to 7 μ above ..... *P. badioconfusa.*

g. Ascosp. hyaline; apoth. exteriorly whitish.
Hym. light brown to dark brown; asci 275 x 12-14 μ; ascosp. minutely warted, 8-10 x 15-17 μ; para. up to 9 μ above, *P. pustulata.*

h. Hym. ferruginous brown; apoth. 1-2 cm in diam. i

h. Hym. dark brown; apoth. 2-3 cm in diam.
Asci 350-380 x 14-16 μ; ascosp. ornamentation very conspicuous, warted, warts up to 1.5 μ high; para. 4-5 μ broad, up to 8-9 μ above ..... *P. brunneoatra.*

i. Ascosp. conspicuously echinulate; apoth. exteriorly yellowish-brown.
Hym. 300-320 μ thick; ascosp. 16-20 x 8-11 μ; para. 3-5 μ broad, slightly enlarged above ..... *P. melaleuca.*

i. Ascosp. inconspicuously verrucose; apoth. exteriorly brown.
Hym. 370-410 μ thick; ect. excipl. 40 μ thick, of text. prism., cells 12-16 x 10-14 μ; med. excipl. 180-246 μ thick, of text. intric., hyphae 2-3 μ broad; ascosp. (14-) 17-21 x 7-9 μ, 2- or 3-guttulate; para. 4-5 μ broad, 7-8 μ above, *P. taxonomic sp.* XI

22. Apoth. strictly coprophilous; asci usually protruding above the hym.; ascosp. surrounded by a mucilaginous sheath ..... *ASCOPHANUS.*

22. Apoth. terri- or lignicolous; asci not protruding above the hym.; ascosp. without a mucilaginous sheath,
HUMARINA and *OCTOSPORA*.

ASCOPHANUS

a. Asci broadly clavate; ascosp. either apiculate or minutely verrucose ..... b.
a. Asci cylindrical; ascosp. neither apiculate nor sculptured ..... c.
b. Ascosp. apiculate, smooth, 35-38 x 11-13 μ (including apiculi).
Hym. whitish or pale yellow; asci 255-285 x 32-40 μ; para. 1-2 μ broad; apoth. disc scattered, globose to scutellate, 0.5-1 mm in diam. ..... *A. holmskjoldii*.
b. Ascosp. non-apiculate, verrucose, 30-33 x 21-23 μ.
Hym. pinkish, asci 225-280 x 40-43 μ; para. 3-4 μ broad; apoth. disc cespitose, discoid, 1-1.5 mm in diam., *A. taxonomic sp.* XII.
c. Para. either strongly enlarged or curved above; apoth. not cespitose ..... d.
c. Para. neither strongly enlarged nor curved above; apoth. cespitose ..... f.
d. Para. not curved but strongly enlarged above ..... e.
d. Para. curved above, 2 μ broad throughout.
Apoth. disc 0.5-1 mm in diam., discoid; hym. ochraceous, 70-90 μ thick; asci 5-7 μ broad; ascosp. ellipsoid, 8-9 x 3-4 μ ..... *A. glaucellus*.
e. Apoth. disc 1-1.5 mm in diam., exteriorly yellow.
Hym. pale yellow, 124-170 μ thick; ascosp. "marked by faint longitudinal striations" Thind *et al.* (1959), narrowly ellipsoid, 12-14 x 4-5 μ; para. 3-4 μ broad, 10-11 μ above, *A. striatus*.
e. Apoth. discs 5-10 mm in diam., exteriorly pale yellow or ochraceous.
Hym. orange-yellow, 120-150 μ thick; ascosp. broadly ellipsoid, 14-15 x 7-8 μ; para. 4-5 μ broad, 12-14 μ above, *A. taxonomic sp.* XIV.
f. Hym. fleshy-red, 160-180 μ thick.
Apoth. discs 0.5-2 mm in diam., exteriorly pink; ascosp. broadly ellipsoid, 13-17 x 7-9 μ; para. 2-4 μ broad, up to 3-5 μ above ..... *A. granulatus*.
f. Hym. ochraceous yellow, 192-210 μ thick.
Apoth. discs pin-head like, 0.5-1(1.5) mm in diam., exteriorly pale yellow or whitish; ascosp. ellipsoid, 16-18 x 8-9 μ; para. 3-4 μ broad, up to 5 μ above ..... *A. ochraceous*.

HUMARINA and *OCTOSPORA*

a. Apoth. up to 2 mm in diam.; hym. pink or orange; ascosp. ellipsoid, smooth walled, 1-guttulate ..... b.
a. Apoth. 2-7 mm in diam.; hym. flesh colored, or ochraceous yellow and turning brown on maturity; ascosp. 1- or 2-guttulate ..... c.

b. Apoth. globose, 1-2 mm in diam.; hym. convex, orange-yellow. Asci cylindrical, 240-260 x 15-18 μ; ascosp. broadly ellipsoid, 20-24 x 10-12 μ; para. 2-3 μ broad, up to 7 μ above; on soil ..... *Octospora convexula.*

b. Apoth. discoid, 0.5-2 mm in diam.; hym. concave, pink to pinkish-violet.
Asci cylindrical, 195-240 x 24-27 μ; ascosp. ellipsoid, 17-19 x 8-10 μ; para. 3-5 μ broad, up to 7 μ above; on sandy soil ..... *Humarina lilacina.* (*sensu* Seaver).

c. Ascosp. 2-guttulate, 16-20 x 8-10 μ; para. 3-4 μ broad, up to 8 μ above. Asci cylindrical, 160-180 x 10-11 μ; apoth. discoid when mature, exteriorly smooth; hym. ochraceous yellow to orange, becoming brown on maturity or on drying; on burnt places ..... *Humarina semiimmersa.* (*sensu* Seaver).

c. Ascosp. 1-guttulate, 17-19 x 9-10 μ; para. 4-5 μ, slightly enlarged above (markedly less than in "c" above).
Asci cylindrical, 240-265 x 14-16 μ; apoth. 2-5 mm, exteriorly tuberculate, with a dentate to crenulate margin; tubercles of text. glob. cells 20-40 μ in diam., some cells transformed into hyaline, unseptate, thin walled projections, such "hairs" 150-170 x 15-18 μ, up to 30 μ broad at the base; hym. pink to flesh colored; on sandy soil, *Octospora taxonomic sp.* XVI.

23. Hairs well developed, gradually tapering to a fine point at the apex, visible to the unaided eye ..... 24.

23. Hairs flexuous and tomentose, or poorly developed, adpressed to the apoth. and with a blunt apex, in either case not visible to the unaided eye ..... 28.

24. Hairs superficial or arising from the med. excipl., the latter usually forked at the base; hym. bright colored, yellow to red when fresh 25.

24. Hairs all superficial, arising from the cells of the ect. excipl.; hym., white, pink, or light yellow ..... 26.

25. Ascosp. smooth, eguttulate, with a thin external sheath or *Coque interperisporique* which separates from the mature spore; hym. yellow or orange-red; plants coprophilous or terricolous . *CHEILYMENIA.*

25. Ascosp. sculptured, guttulate, *Coque interperisporique* remaining permanently as a part of the ascosp. wall; hym. orange red to scarlet-red; plants lignicolous or terricolous ..... *SCUTELLINIA.*

CHEILYMENIA

a. Ascosp. large, more than 16 μ long ..... b.

a. Ascosp. small, 10-12 μ long.
Apoth. 1-2 mm in diam.; hairs forked and much swollen at the base, 400-600 x 14-18 μ, 20-30 μ at the base; asci 225-265 x 10-13 μ; ascosp. ellipsoid, 10-12 x 7-8 μ; para. 3-4 μ broad, up to 7-8 μ at the apex .... *C. taxonomic sp.* XVII.

b. Hairs brown, forked or palmately branched at the base ..... c.

b. Hairs subhyaline, usually not forked at the base.
Apoth. 3-5 mm in diam.; hairs 300-500 x 10-16 μ; asci 200-260 x 10-12 μ; ascosp. broadly ellipsoid, (14-)16-18 x 9-10 μ; para. 2-3 μ broad, up to 6 μ at the apex,
C. theleboloides.

c. Apoth. 0.5-0.8 mm in diam.; hairs small, 300-400 x 8-10 μ, up to 17 μ near the base.
Ect. excipl. cells 30-60 x 25-40 μ; asci 200-250 x 10-12 μ; ascosp. 20-25 x 11-13 μ; para. 2-3 μ, up to 6 μ at the apex,
C. pulcherrima.

c. Apoth. larger than 1 mm ..... d.

d. Apoth. 5-6 mm in diam.; hairs large, 500-800 x 15-20 μ, up to 40 μ near the base and forked ..... *C. coprinaria.*

d. Apoth. 0.8-2.5 mm in diam.; hairs palmately branched at the base, up to 1000 μ long, 15-25 μ wide ..... *C. stercorea.*

SCUTELLINIA

a. Apoth. 2-12 mm in diam.; ascosp. sculptured, sculpturing consisting of minute to conspicuous warts ..... b.

a. Apoth. 0.5-1 mm in diam.; ascosp. smooth walled.
Medullary hairs septate, brown, 200-300(-450) x 10-15 μ; asci 225-275 x 7-8 μ; ascosp. 12-14 x 6-7 μ; para. 2-3 μ broad, not conspicuously enlarged above ..... *S. pygmea.*

b. Hairs much longer than 200 μ, septate, usually forked at the base and pointed at the apex; on wood or soil ..... c.

b. Hairs 150-200 μ long, non-septate; on mud or soil.
Apoth. 2-7 mm in diam.; medullary hairs abundant; ascosp. broadly ellipsoid, walls warted, warts 1-2 μ high, 1-guttulate, 20-25 x 12-15 μ ..... *S. uliginosa.*

c. Ascosp. 21-23 x 11-13 μ, minutely warted, warts rounded, 0.5-1.5 μ high, 1- or 2-guttulate.
Apoth. usually 5-10 mm in diam., occasionally smaller; medullary hairs dark brown, 300-700 x 30-40 μ; excipl. hairs present, much smaller in dimensions; para. 3-4 μ broad, up to 10 μ above; on rotten wood, twigs or leaves, rarely on rotten perennial polypores ..... *S. scutellata.*

c. Ascosp. (15-)19-20 x 11-13 μ, ellipsoid, ornamentations of warts up to 1 μ thick, 1-guttulate.
Apoth. 2-5 mm in diam., rarely somewhat larger; medullary hairs 800-1800 x 25-40 μ, brown, forked at the base; excipl. hairs absent; para. 3-5 μ broad, up to 8 μ above; on soil,
S. cubensis.

26. Hairs dark brown; apoth. cupulate or discoid; ascosp. smooth or sculptured ..... 27.

26. Hairs hyaline; apoth. discoid; ascosp. smooth.
Apoth. disc 0.5-1 mm in diam., exteriorly cream-white or with a pinkish tint; hym. pink, 125-150 μ thick; asci 21-24 μ broad, J-negative; ascosp. hyaline, smooth walled, with a mucilaginous sheath, 16-18 x 10-12 μ; para. 2-3 μ broad, slightly enlarged above; hairs non-septate, 265-300 x 18-24 μ; on horse dung,
LASIOBOLUS equinus.

27. Apoth. discoid, less than 1 cm in diam.; ascosp. smooth or sculptured ..... 29.

27. Apoth. disc cupulate, 2-3 cm in diam., 1-1.5 cm deep; ascosp. sculptured.

Apoth. exteriorly dark brown, densely hairy, hairs 1-1.5 mm x 20-30 μ; hym. white or cream colored, 200-250 μ thick; ascosp. 2-guttulate, 19-24 x 12-13 μ; para. 3-5 μ broad, up to 6 μ above; on soil ..... *HUMARIA hemispherica.*

28. Hym. provided with setae as well as paraphyses, apoth. occurring on pine needles ..... *Desmazierella acicola.*

28. Hym. without setae, apoth. not occurring on pine needles ..... 30.

29. Ascosp. guttulate ..... *TRICHOPHAEA.*

29. Ascosp. eguttulate.

Ascosp. (16-) 20-23 x 9-11 μ; apoth. disc 4-7 mm in diam., exteriorly light brown; hym. greyish brown ..... *TRICHARIA gilva.*

TRICHOPHAEA

a. Ascosp. globose, 1-guttulate; apoth. shallow cupulate, becoming discoid; hym. pinkish, becoming light brown ..... b.

a. Ascosp. ellipsoid, 1- or 2-guttulate; apoth. deep cupulate; hym. cream-white ..... c.

b. Plants occurring on soil; hym. light brown; para. swollen above (up to 7 μ) ..... *T. brunnea.*

b. Plants occurring on burnt places; hym. pink to reddish; para. slightly enlarged above (up to 4 μ) ..... *T. tuberculata.*

c. Ascosp. smooth walled.

Ascosp. distinctly 2-guttulate, 23-25 x 9-10 μ; apoth. disc 4-7 mm in diam.; hairs aggregated in clusters, brown, 200-300 x 16-20 μ; hym. cream-white, becoming light brown; asci 240-280 x 12-14 μ; para. 3 μ broad, not enlarged above ..... *T. albospadacea.*

c. Ascosp. sculptured.

Ascosp., sculpturing consisting of small warts, 16-19 (-21) x 8-9 μ, 1-guttulate; apoth. disc 3-5 mm in diam.; hairs aggregated, light brown, 200-350 x 10-14 μ; hym. cream-white; para. 2-3 μ broad, up to 6 μ above ..... *T. gregaria.*

30. Hairs dark brown, inconspicuous, straight, often falling off; apoth. shallow discoid on maturity ..... 31.

30. Hairs light brown or subhyaline, flexuous, conspicuous, apoth. deep cupulate, subhypogeous; ascosp. smooth ..... *SEPULTARIA.*

SEPULTARIA

(Identification of species of *Sepultaria* is confused, and these are tentative taxonomic conclusions based on the descriptions in most of the monographs. Jules Favre (1955—Les Champignons Superieurs de la Zone Alpine du Parc National Suisse, pp. 1-212, Liestal) sketches ascospores from the type material of *S. arenosa* Fuckel as nonguttulate.)

a. Ascosp. 1-guttulate, 25-28 x 12-14 μ; apoth. (1-)2-4 cm in diam.; hym. pale yellow ..... *S. arenicola.*

a. Ascosp. 2-guttulate, 20-24 x 8-10 μ; apoth. 0.5-1 cm in diam.; hym. whitish ..... *S. arenosa.*

31. Apoth. disc and hym. scarlet red, 2-5 cm in diam.; on eroded soil, *ALEURIA rubra.*
(See lead 20.)

31. Apoth. disc exteriorly brown, 4-5 mm in diam.; hym. light buff to brownish; on burnt ground.
Superficial hairs present, dark brown, septate, 100-150 x 5-7 μ; outer few layers of ect. excipl. of text. prism., inner layers of text. glob., cells of ect. excipl. 18-30 x 14-22 μ; med. excipl. of text. intric., hyphae 2-3 μ broad; hym. 240-296 μ thick; ascosp. narrowly ellipsoid, 1-guttulate, 21-25 x 8-10 μ; para. 3-4 μ broad, slightly enlarged above ..... *ANTHRACOBIA melaloma.*

NEW TAXA AND NEW COMBINATIONS

Octospora cacaina (Thind, Cash & Sethi) L. Batra, comb. nov.
≡ *Humarina cacaina* Thind, Cash & Sethi, Mycologia 49:833. 1957.

Octospora convexula (Pers. ex Fr.) L. Batra comb. nov.
≡ *Peziza convexula* Pers. ex Fr., Syst. Myc. p. 73. 1823.
≡ *Humarina convexula* (Pers. ex Fr.) Seaver, North Amer. Cup-fungi p. 128. 1928.

Pulvinula carbonaria (Fuckel) Boudier var. *brevispora* L. Batra, var. nov. *Ascosporae praviores quam P. carbonaria* (Fuckel) Bouider var. *typica,* Hist. Class. Discomyc. Eur. P. 70. 1907.

Pulvinula discoidea (P. Henn. & E. Nym.) L. Batra, comb. nov.
≡ *Barlaea discoidea* P. Henn. & E. Nym., Monsunia 1:33. 1900.

Pulvinula mussooriensis (Thind, Cash & Singh) L. Batra, comb. nov.
≡ *Lamprospora mussooriensis* Thind, Cash & Singh, Mycologia 51:457. 1959.

Trichophaea brunnea (Alb. & Schw. ex Fr.) L. Batra, comb. nov.
≡ *Peziza brunnea* Alb. & Schw. ex Fr., Syst. Myc. p. 83. 1823.

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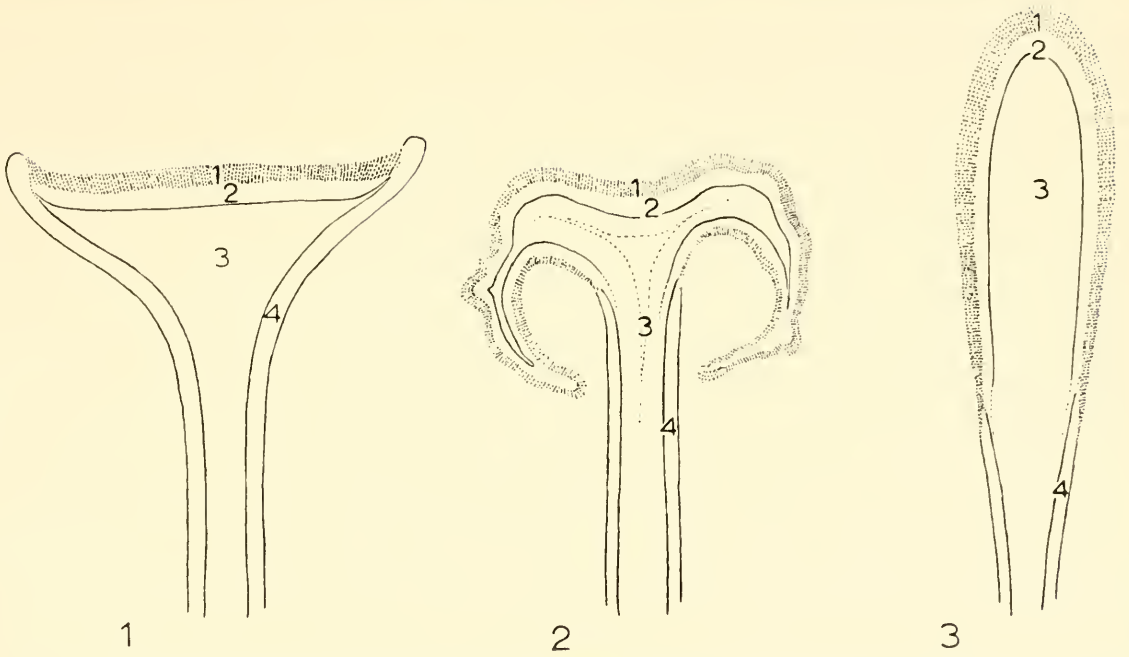


Fig. 1.—A median longitudinal section through a cupulate apothecium showing various tissue zones (diagrammatic).

Fig. 2.—A median longitudinal section through a mitrate apothecium showing various tissue zones (adapted from an actual photomicrograph of *Leotia lubrica* Scop. *ex* Fr.)

Fig. 3.—A median longitudinal section through a terete or spathulate apothecium showing various tissues (adapted from actual photomicrograph of *Geoglossum* sp.).

The numbers inside the drawings indicate various tissue zones in the apothecium: 1 = hymenium; 2 = subhymenium; 3 = medullary excipulum or medulla; 4 = ectal excipulum.

FIGURES 4-13 (Camera lucida drawings)

FIGS. 4-6.—*Lamprospora multiguttula* Batra.

FIG. 4.—An ascus and a paraphysis, × 500.

FIG. 5.—L. S. of an apothecium showing hymenium, subhymenium, medullary excipulum and ectal excipulum, × 130.

FIG. 6.—Ectal excipulum, × 500.

FIGS. 7-8. *Lamprospora chopraina* Batra.

FIG. 7.—An ascus with ascospores and a paraphysis, × 500.

FIG. 8.—L. S. of an apothecium showing apothecial margin, ectal excipulum and a part of medullary excipulum, × 500.

FIGS. 9-10.—*Plicaria papillosa* Batra.

FIG. 9.—L. S. of an apothecium showing a papilla of ectal excipulum and a part of medullary excipulum which is indistinguishable from the former except for the direction of the cells, × 500.

FIG. 10.—Ascospores, × 1100.

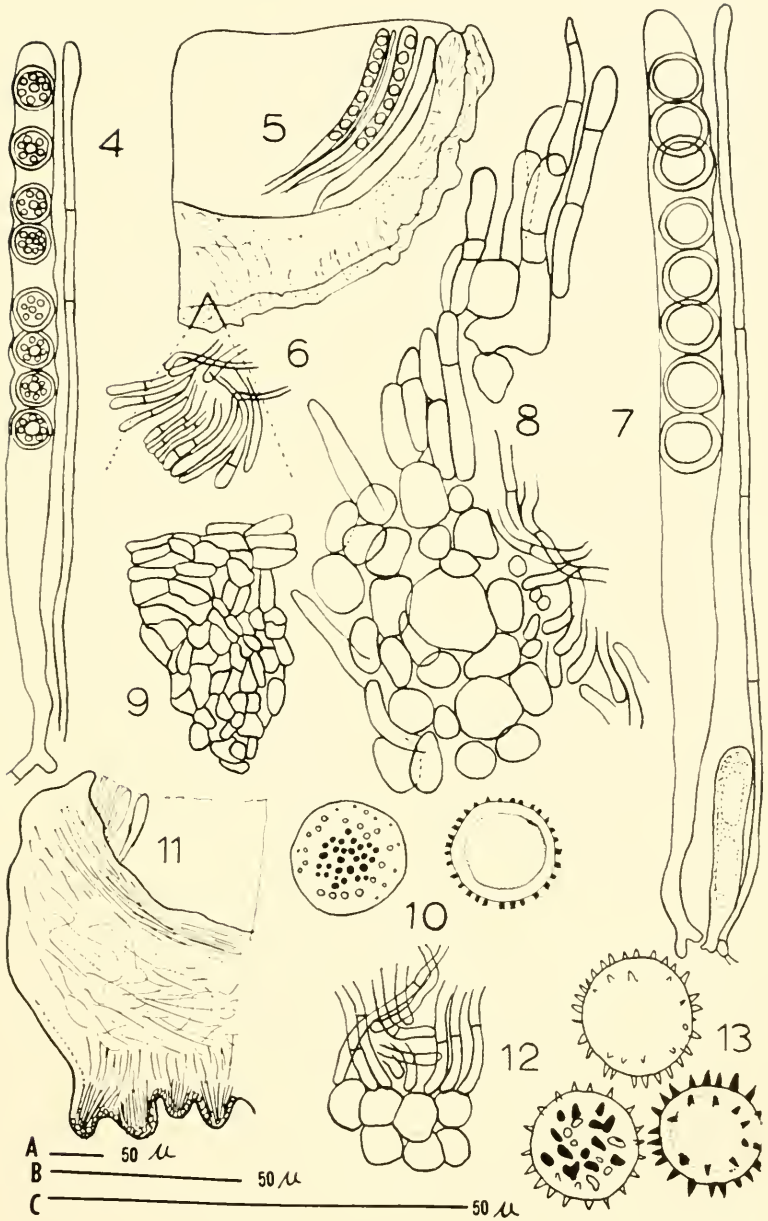
FIGS. 11-13.—*Plicaria pseudoplanchonis* Batra.

FIG. 11.—L. S. of an apothecium showing general outline of various tissues, × 130.

FIG. 12.—Ectal excipulum and a part of medullary excipulum, × 500.

FIG. 13.—Ascospores, × 1100. Scale A for Fig. 5, 11; scale B for the Figs. 4, 7, 9, 12; scale C for Figs. 10, 13. All the figures are drawn with the aid of a camera lucida.

FIGURES 4-13 (Camera lucida drawings)



FIGURES 14-20 (Camera lucida drawings)

FIGS. 14-16.—*Aleuria rubra* Batra.

Fig. 14.—Part of a L. S. of apothecium, ectal and part of medullary excipulum, × 500.

FIG. 15.—Upper portion of paraphyses, × 500.

FIG. 16. Ascospores, × 1100.

FIGS. 17-20. *Scutellinia uliginosa* Batra.

FIG. 17.—Ascospores, × 1100.

FIG. 18.—L. S. of apothecium showing hymenium, subhymenium, medullary excipulum and ectal excipulum, × 130.

FIG. 19.—Part of ectal excipulum at higher magnification, × 500.

FIG. 20. An ascus and a paraphysis, × 500. Scale A for Fig. 18; scale B for Figs. 14, 15, 19, 20; scale C for Figs 16, 17.

FIGURES 14-20 (Camera lucida drawings)

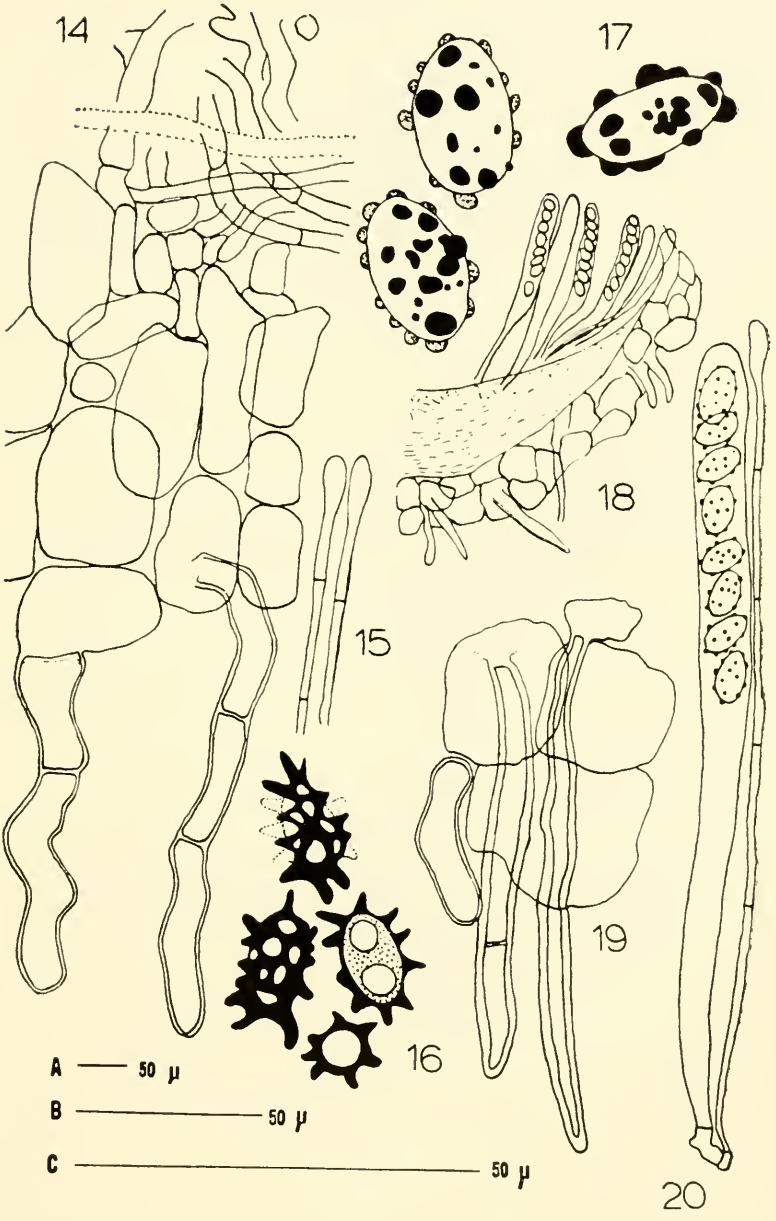
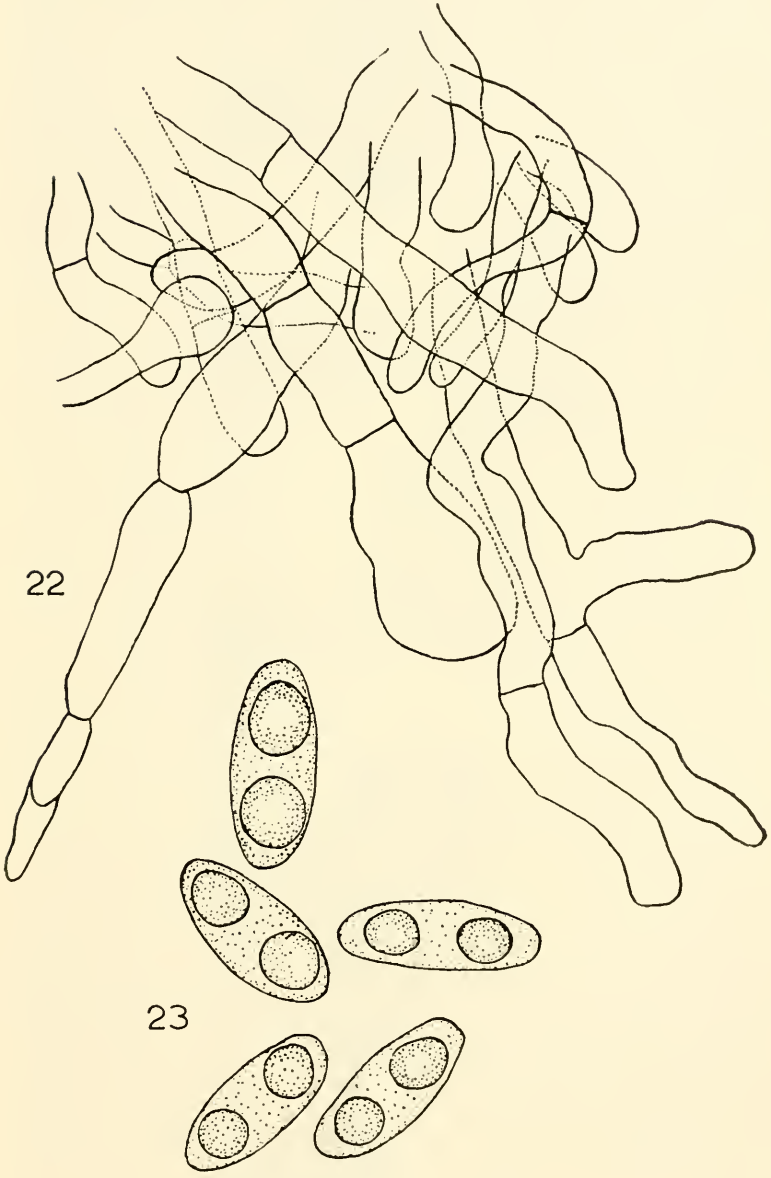


FIGURE 21

Gyromitra infula (Schaeff. *ex* Fr.) Quél.

FIG. 21.—External appearance of apothecia (approx. nat. size).

FIGURES 22, 23 (Camera lucida drawings)



Gyromitra infula Scop. *ex* Fr.

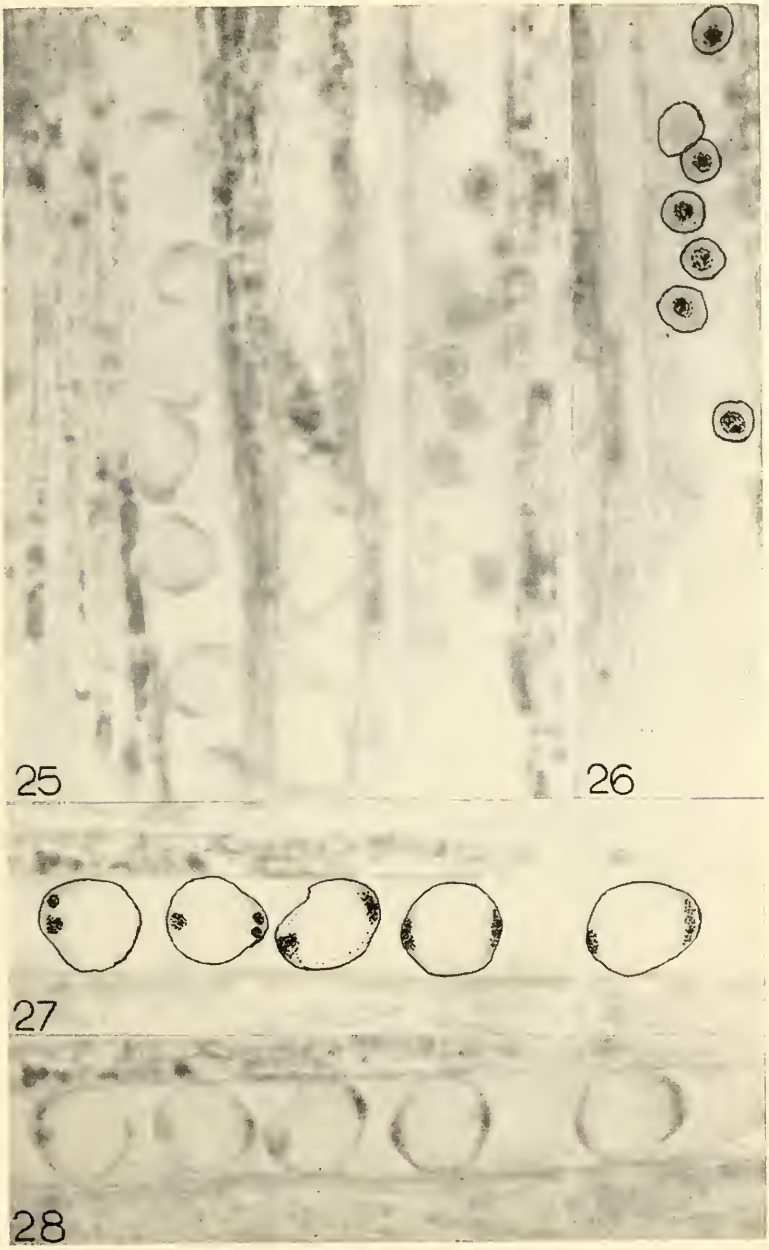
FIG. 22.—Portion of ectal excipulum made up of textura intricata, × 500.
FIG. 23.—Ascospores, × 700.

FIGURE 24

Helvella acetabulum (L. *ex* Fr.) Quél.

FIG. 24.—Apothecia showing general morphology (approx. nat. size).

FIGURES 25-28 (×1000, material stained with Haematoxylin)



Helvella acetabulum (L. *ex* Fr.) Quél.

Fig. 25.—Photomicrograph of some stages in ascospore development.

Fig. 26.—Same as fig. 25, with ascospore and nuclei indicated with India ink.

Fig. 27.—Sections of mature ascospores showing nuclei. India ink drawing of spores shown in fig. 28.

Fig. 28.—Photomicrograph of mature ascospores.

FIGURES 29, 30

Helvella atra König *ex* Fr.

FIG. 29.—Apothecia showing general morphology of mature plants (approx. nat. size).

FIG. 30.—Mature apothecia showing variation in form and size.

FIGURES 29, 30

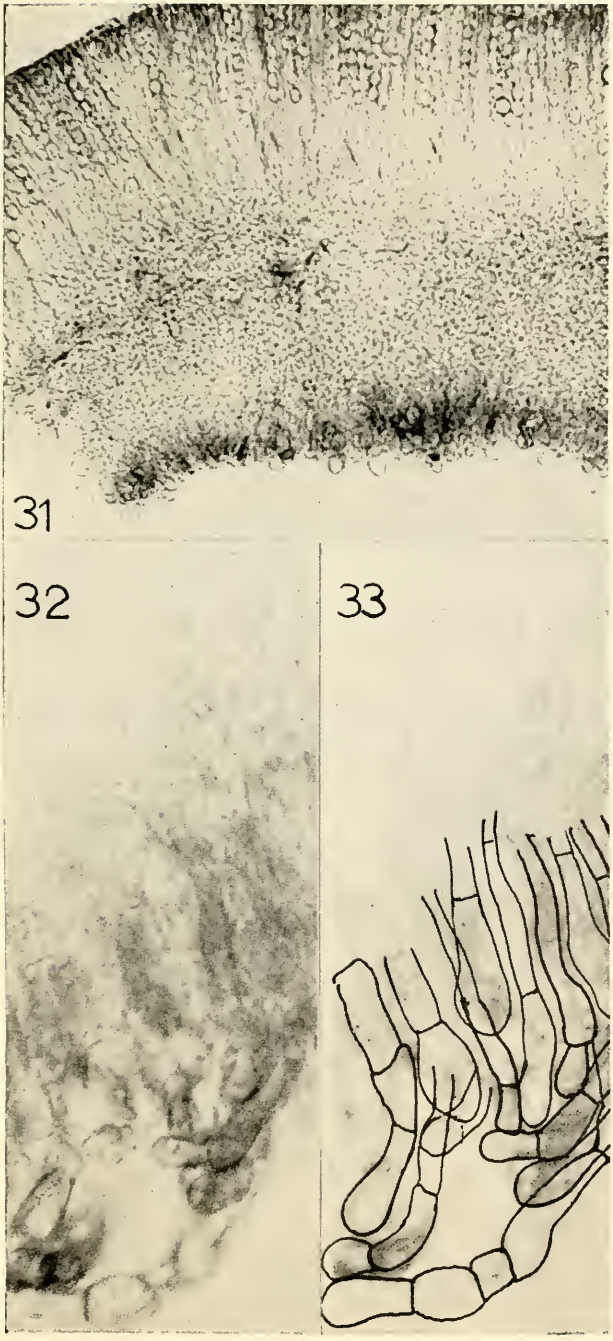
FIGURES 31-33

Helvella atra König *ex* Fr.

FIG. 31.—L. S. of apothecium showing hymenium, medullary and ectal excipulum, × 100.

FIG. 32, 33.—L. S. through ectal excipulum, × 500.

FIGURES 31-33

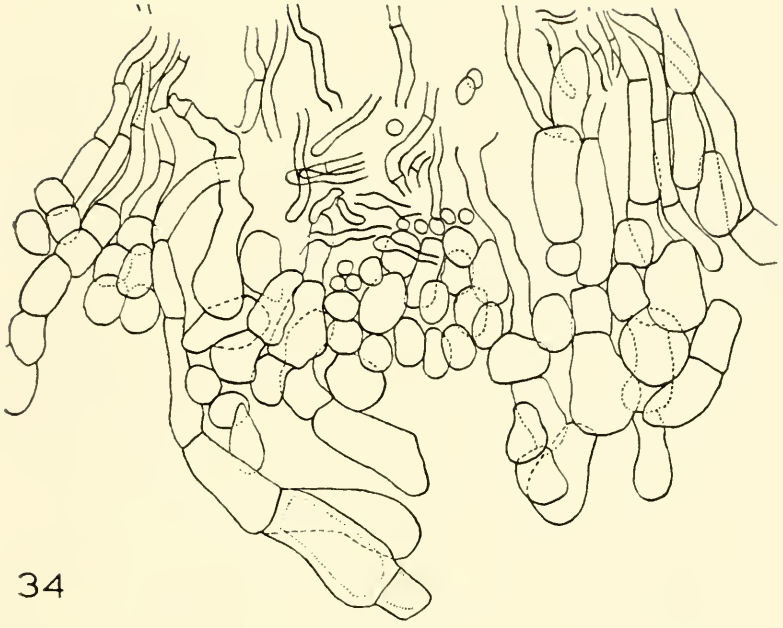


FIGURES 34, 35

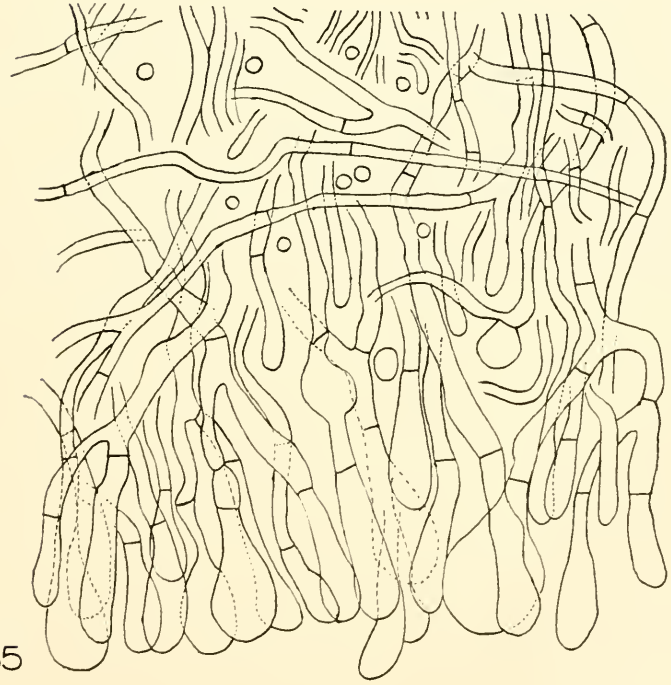
FIG. 34.—*Helvella acetabulum* (L. *ex* Fr.) Quél. L. S. through ectal excipulum and a portion of medullary excipulum, camera lucida drawing, × 500.

FIG. 35.—*H. atra* König. L. S. through ectal excipulum and a portion of medullary excipulum, camera lucida drawing, × 500.

FIGURES 34, 35



34



35

FIGURES 36-38 (all camera lucida drawings × 500)

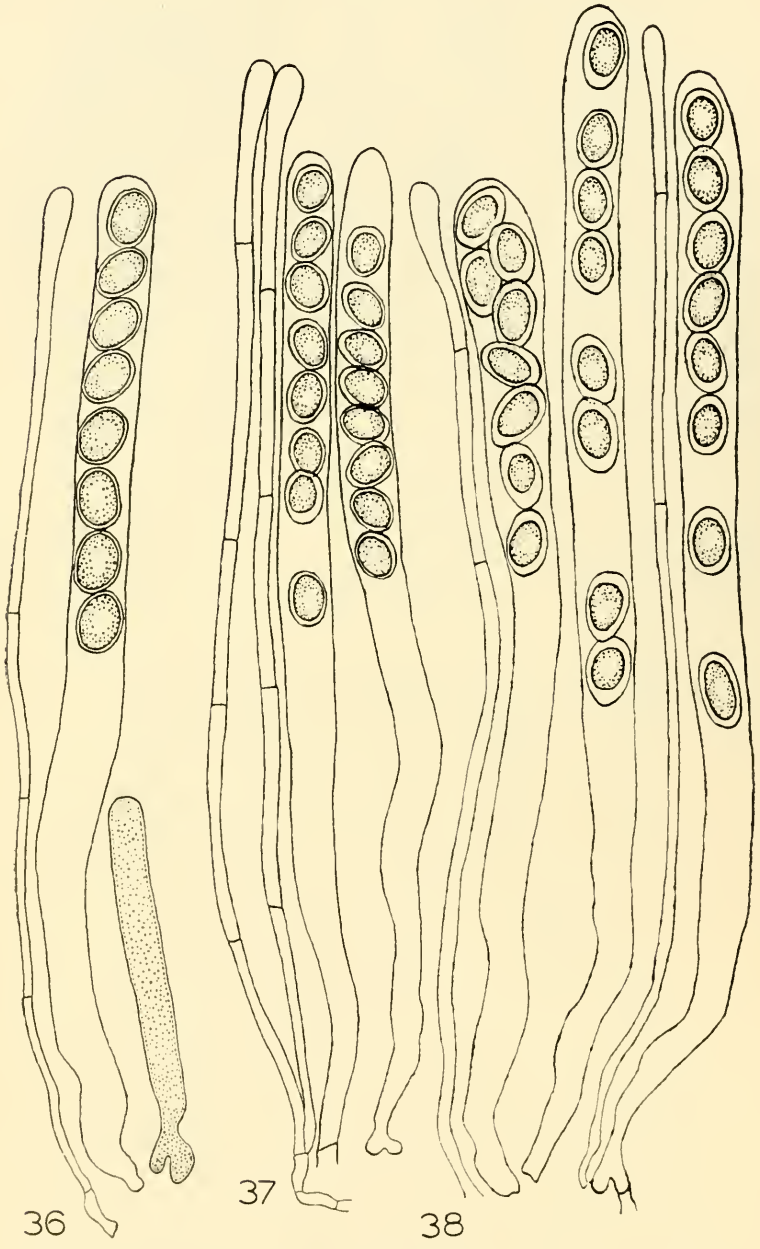


FIG. 36.—*Helvella acetabulum* (L. *ex* Fr.) Quél., asci and a paraphysis.
FIG. 37.—*H. atra* König, asci and paraphyses.
FIG. 38.—*H. calyciformis* Batt. *ex* Quél., asci and paraphyses.

FIGURE 39

Helvella crispa Scop. *ex* Fr.

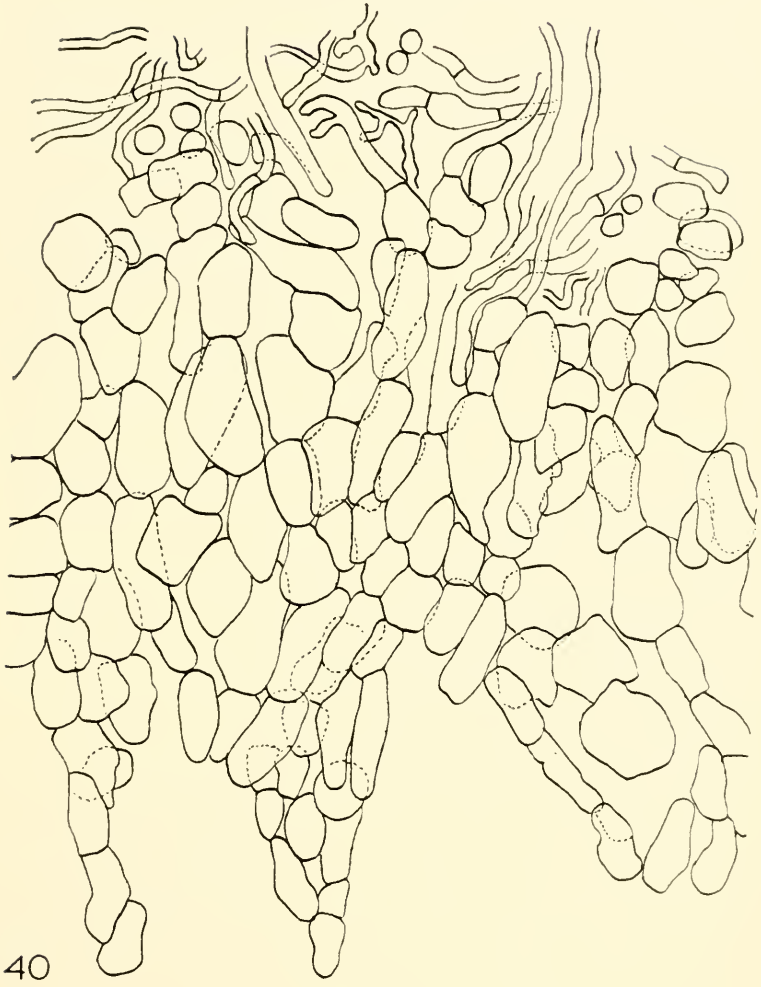
FIG. 39.—Apothecia showing external appearance and variation. Note distinct grooves and ridges (approx. nat. size).

FIGURE 40

Helvella crispa Scop. *ex* Fr.

FIG. 40.—L. S. through ectal excipulum and part of medullary excipulum (camera lucida drawing × 500).

FIGURE 40



FIGURES 41-43

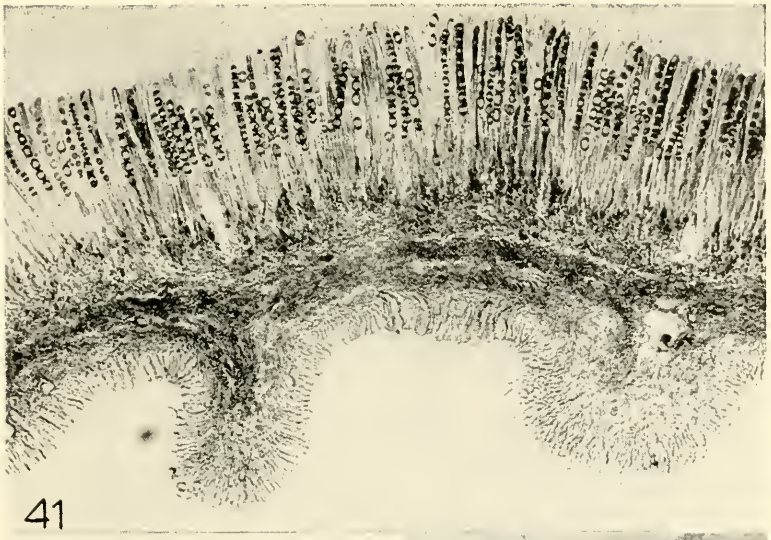
Helvella calyciformis Batt. *ex* Quél.

FIG. 41.—Photomicrograph of L. S. through the middle of an apothecium showing hymenium, subhymenium, medullary and ectal excipulum, free-hand section, stained in Phloxine, × 100.

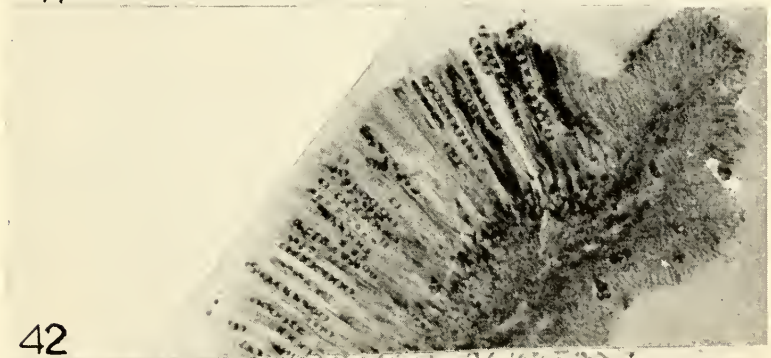
FIG. 42.—Photomicrograph of a L. S. through the margin of an apothecium, free-hand section, stained in Cotton Blue, × 100.

FIG. 43.—Photomicrograph of a L. S. through ectal excipulum in one of the ridges, × 500.

FIGURES 41-43



41



42

43

FIGURES 44-46

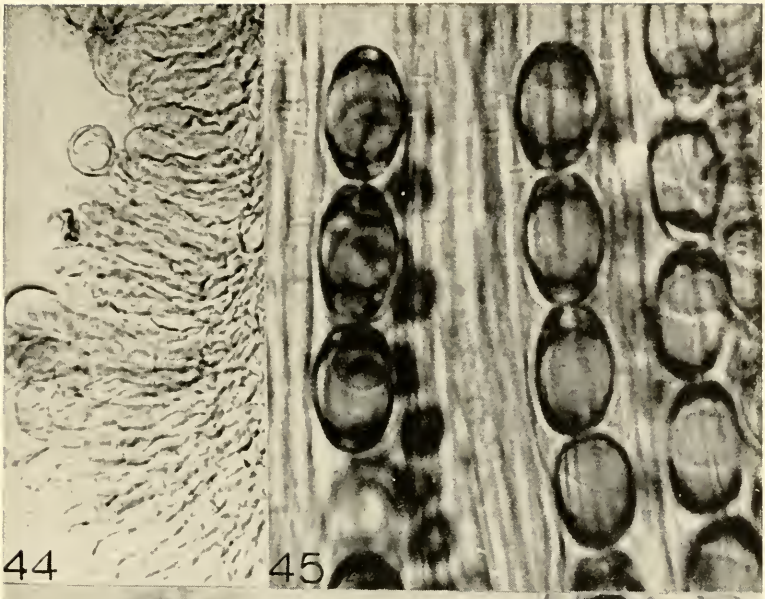
Helvella calyciformis Batt. *ex* Quél.

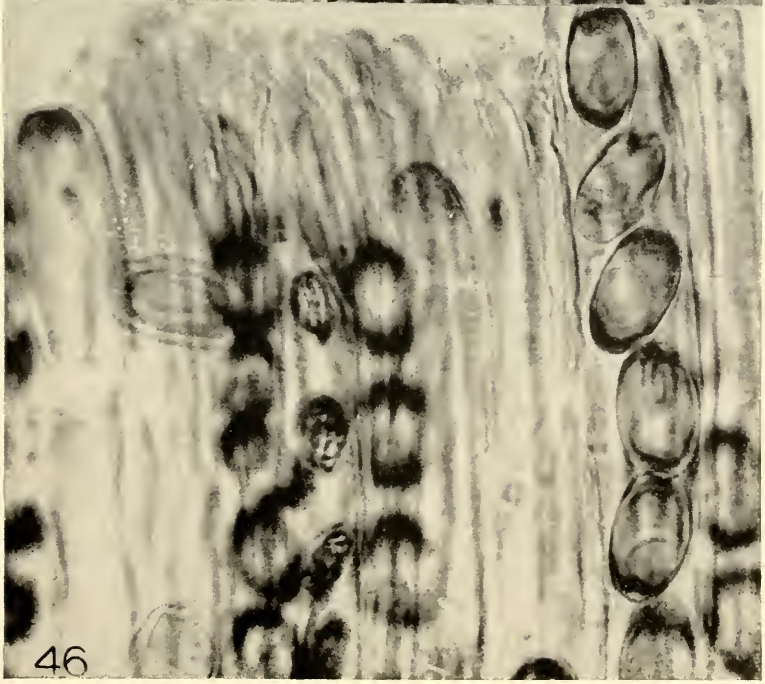
FIG. 44.—Photomicrograph of a section through one of the apothecial ridges showing columnar cells of ectal excipulum, × 500.

FIG. 45.—Photomicrograph of ascospores stained with Cotton Blue, × 500.

FIG. 46.—Photomicrograph of L. S. through hymenium showing asci, paraphyses and ascospores, stained with Cotton Blue, × 500.

FIGURES 44-46





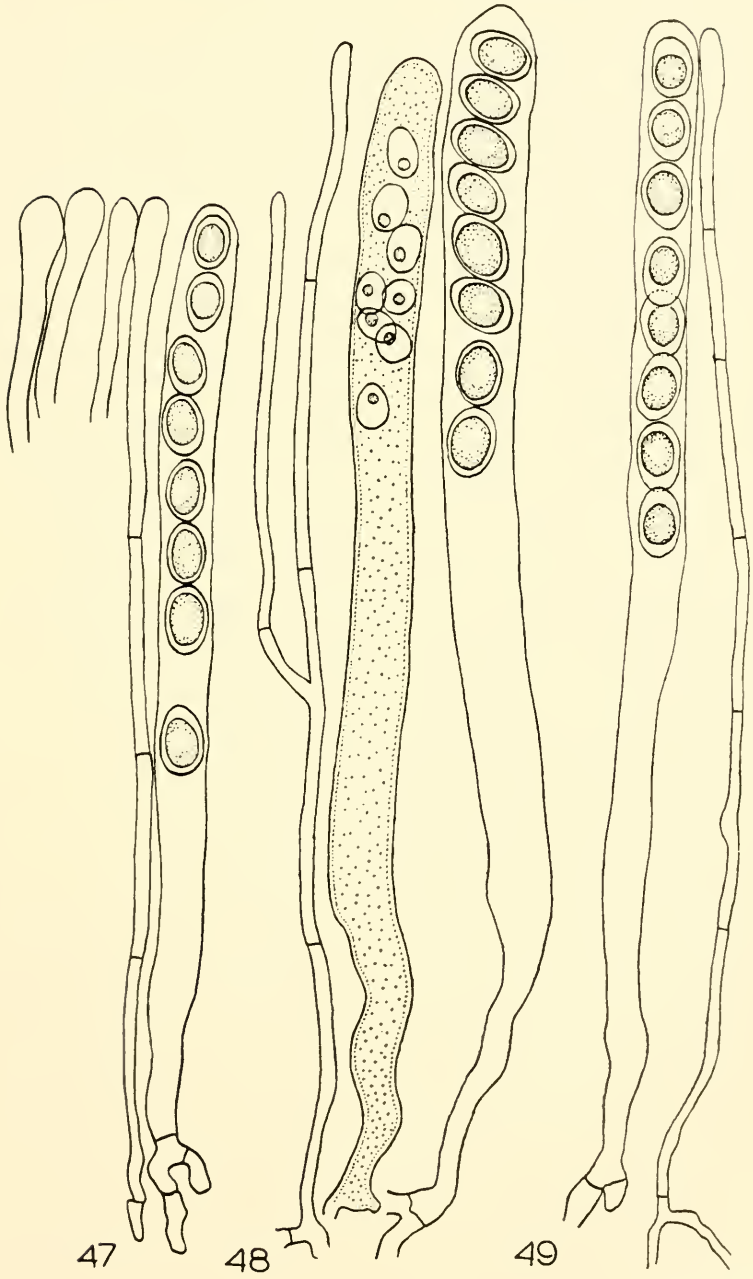
FIGURES 47-49

FIG. 47.—*Helvella crispa* Scop. *ex* Fr., an ascus and paraphyses.

FIG. 48.—*H. elastica* Bull. *ex* Fr., asci and paraphysis.

FIG. 49.—*H. ephippium* Quél., an ascus and a paraphysis.

FIGURES 47-49 (Camera lucida drawings × 500)

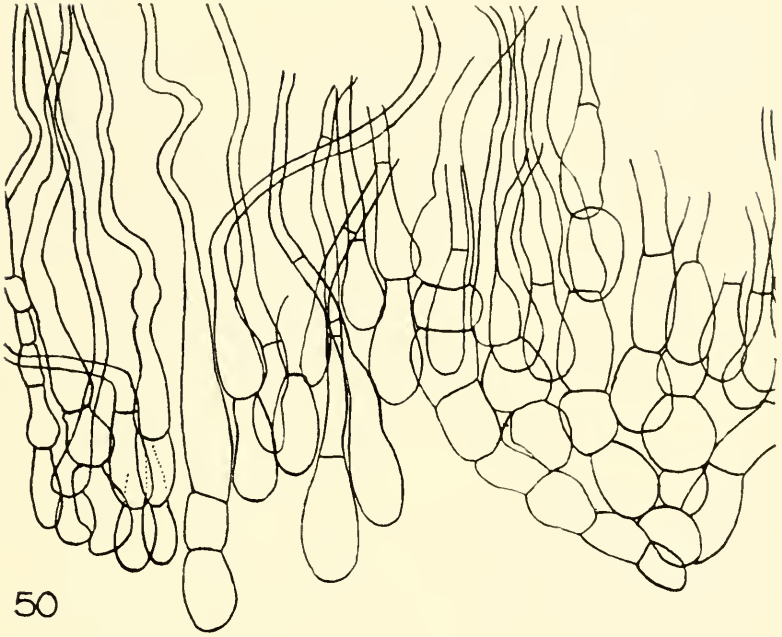


FIGURES 50, 51

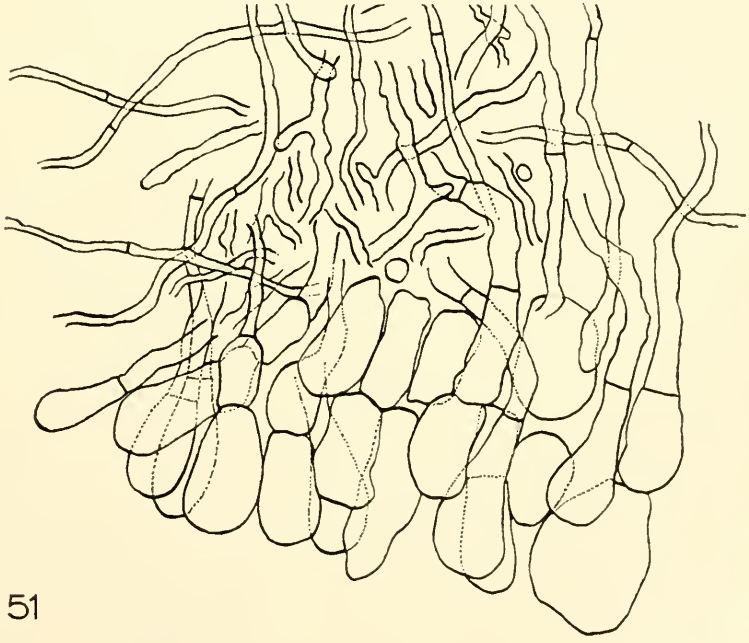
FIG. 50.—*Helvella calyciformis* Batt. *ex* Quél., ectal excipulum and a portion of medullary excipulum.

FIG. 51.—*H. elastica* Bull. *ex* Fr., ectal excipulum and a portion of medullary excipulum.

FIGURES 50, 51 (Camera lucida drawings × 500)



50



51

FIGURES 52, 53

Helvella elastica Bull. *ex* Fr.

FIG. 52.—Apothecia showing even stipe and saddle shaped pileus (approx. nat. size).

FIG. 53.—Apothecia showing variation in form and size (approx. nat. size).

FIGURES 52, 53

FIGURES 54-56

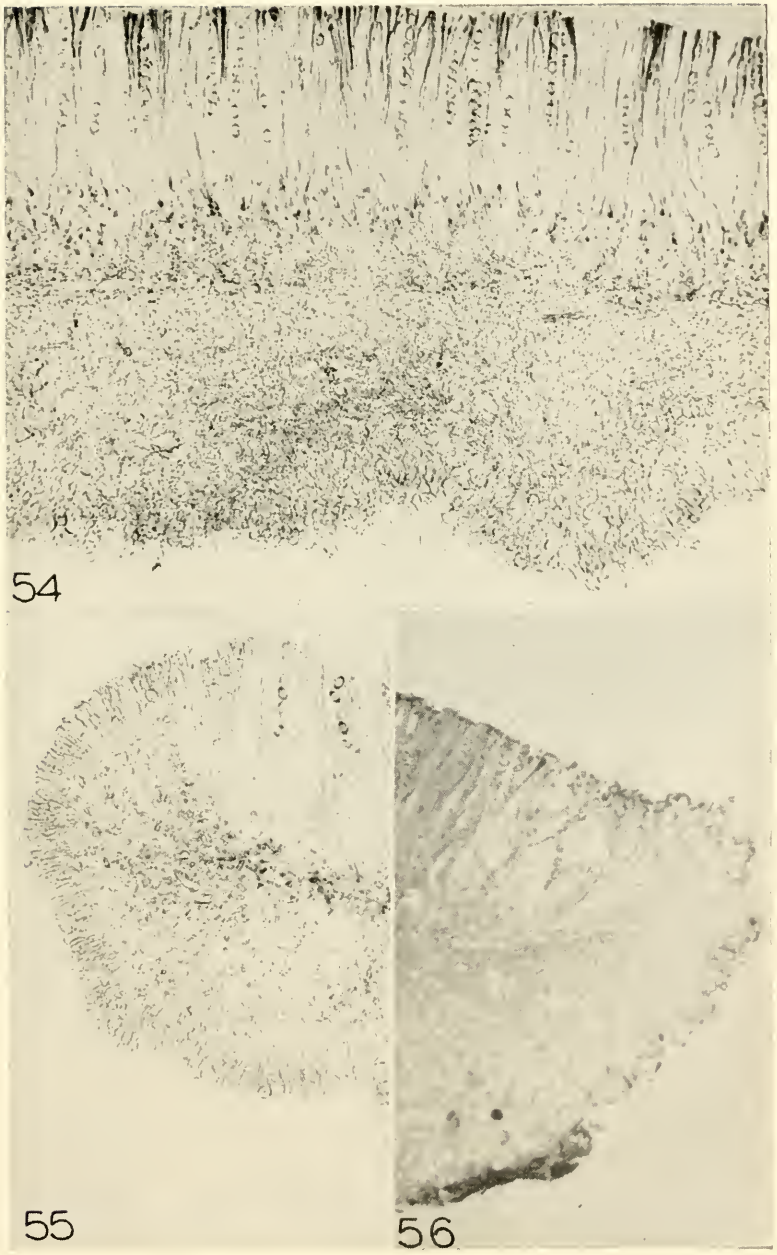
Helvella elastica Bull. *ex* Fr.

FIG. 54.—Photomicrograph of L. S. through middle of pileus. Material *ex* type *Helvella gracilis* Peck, freezing microtome, stained with Cotton Blue, × 100.

FIG. 55.—Photomicrograph of L. S. through the margin of pileus. Material *ex* type *Helvella gracilis* Peck, freezing microtome, stained with Cotton Blue, × 100.

FIG. 56.—Photomicrograph of L. S. through the margin of pileus, freezing microtome, stained with Haematoxylin, × 100.

FIGURE 54-56



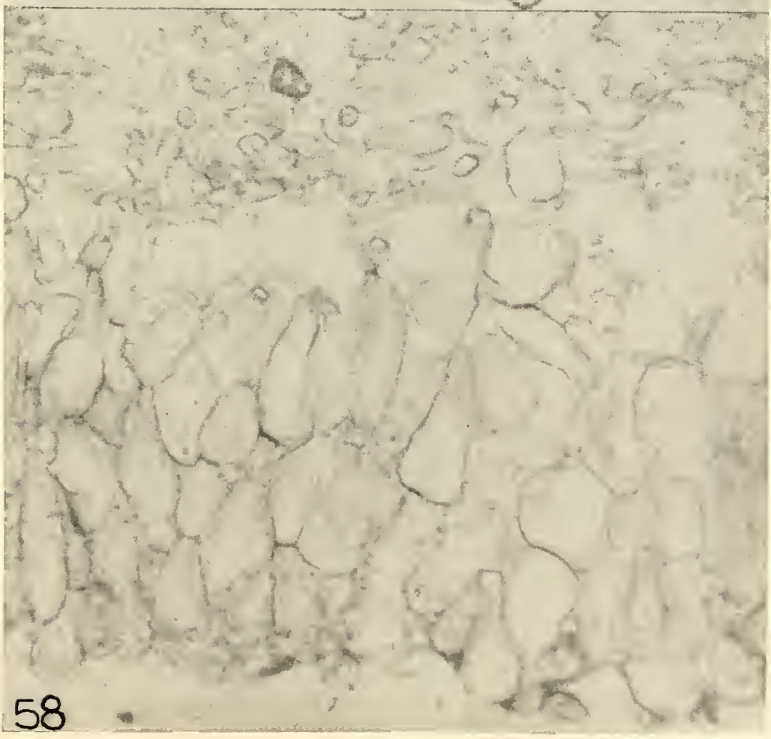
FIGURES 57, 58

Helvella elastica Bull. *ex* Fr.

FIG. 57.—Photomicrograph of L. S. through ectal excipulum of pileus, freezing microtome, stained with Cotton Blue, × 500.

FIG. 58.—Photomicrograph of L. S. through ectal excipulum of pileus, stained with Haematoxylin, × 500.

FIGURES 57, 58



FIGURES 59-66

Helvella elastica Bull. *ex* Fr.

FIG. 59.—Photomicrograph of a young ascus and developing ascospores.

FIG. 60.—Same stage as in Fig. 59, outlined with India ink.

FIG. 61—Same ascospores showing two distinct nuclei near each end.

FIG. 62.—Same stage as in Fig. 61, outlined with India ink.

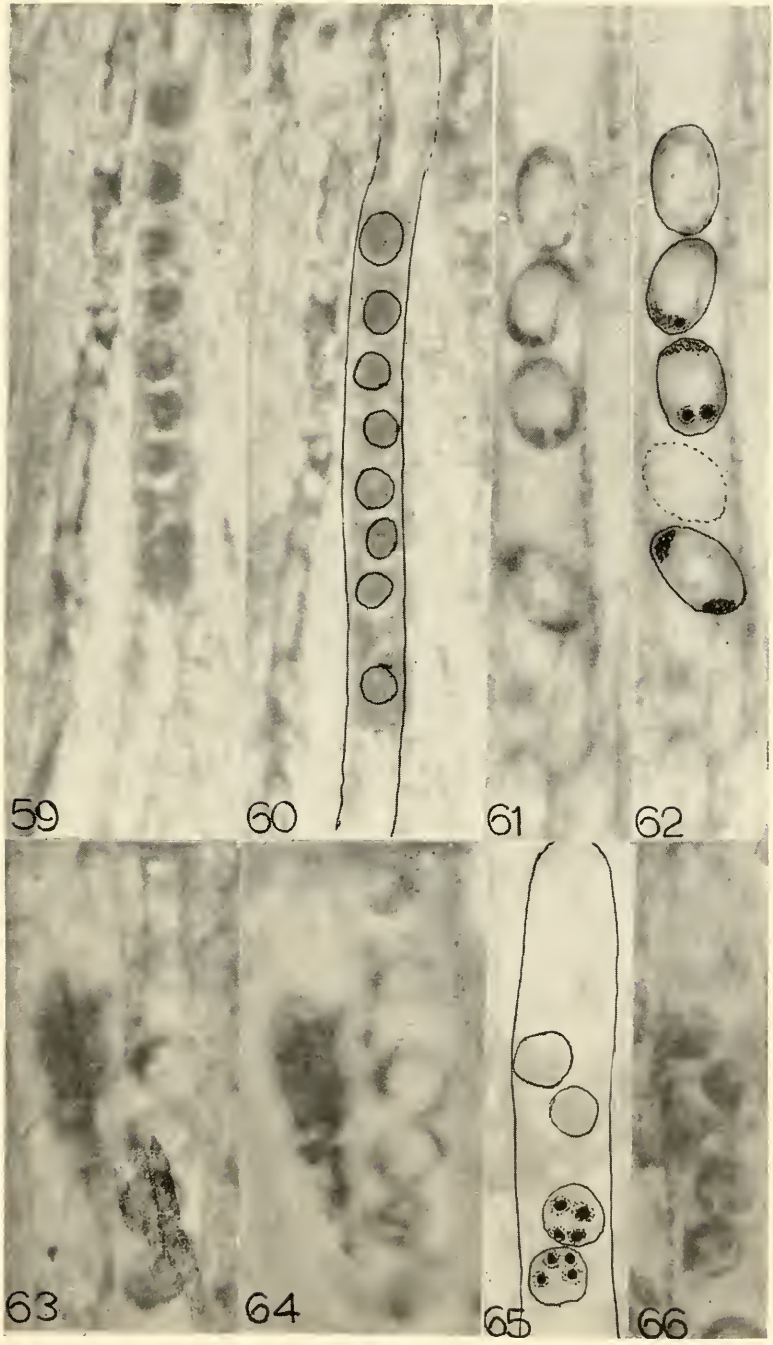
FIG. 63, 64.—Ascospores, one of which shows two nuclei of one end, the two nuclei of the other end shown in the following serial section in Fig. 64.

FIG. 65, 66.—Two of the four ascospores showing four nuclei each.

FIG. 65.—Nuclei outlined with India ink.

FIG. 66.—Actual photomicrograph.

FIGURES 59-66 (Photomicrographs, material stained in Haematoxylin, all × 1000)



FIGURES 67-77

Helvella elastica Bull. *ex* Fr.

FIG. 67.—An ascus showing 4-nucleate ascospores.

FIG. 68.—Same stage as in Fig. 67, outlined in India ink.

FIG. 69.—An ascus showing 8 mature ascospores with the two nuclei from each end fused and forming typical moon-shaped nuclei.

FIG. 70.—Same stage as in Fig. 69, upper ascospore outlined in India ink.

FIG. 71.—An ascus showing 8-spores with two moon-shaped nuclei at each end.

FIG. 72-77.—Ascospores showing small warts on the epispore. Some of the warts are interlaced with minute ridges.

FIGURES 67-77 (Material stained with Haematoxylin all fig. $\times$ 1000).

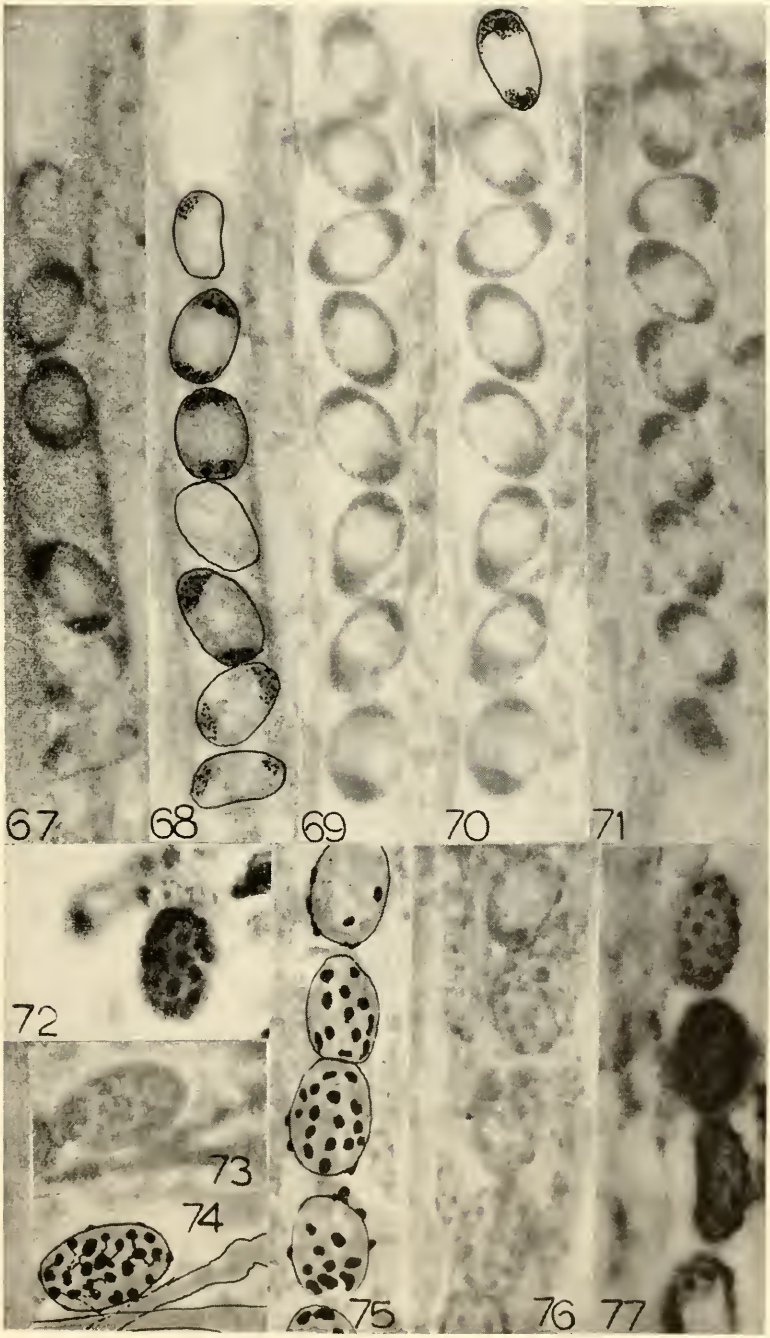
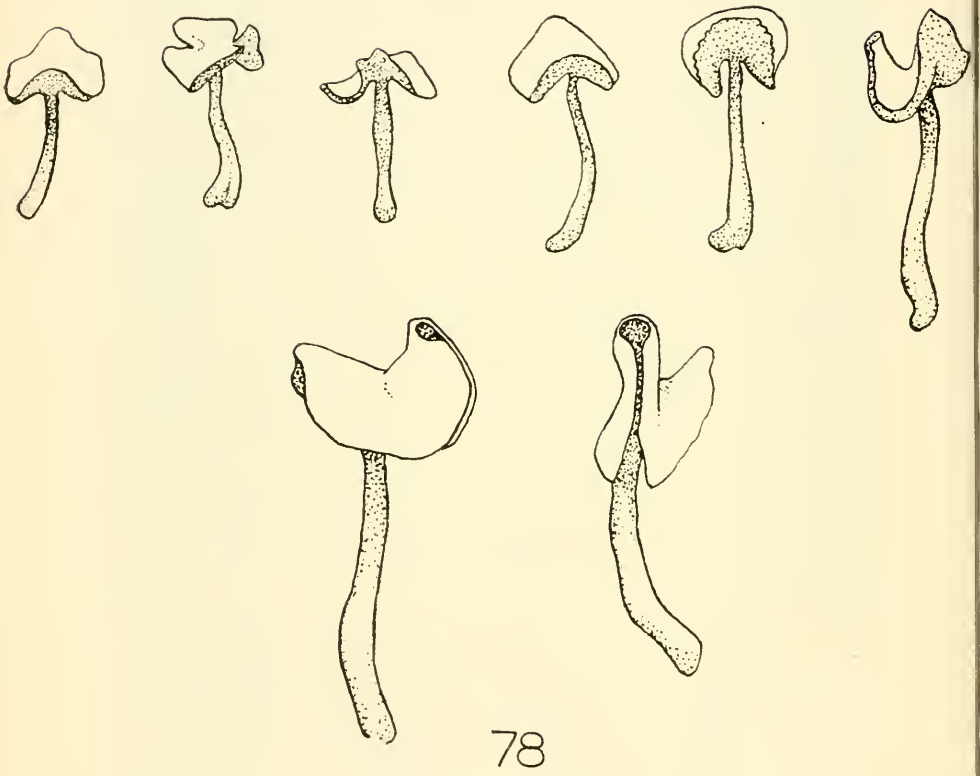


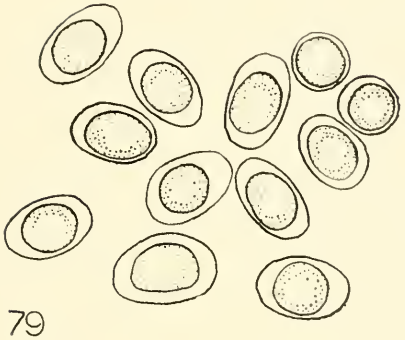
FIGURE 78



Helvella ephippium Lév.

FIG. 78.—Apothecia showing variation in size and form, free-hand drawings from fresh specimen (approx. n.t. size).

FIGURES 79, 80



79

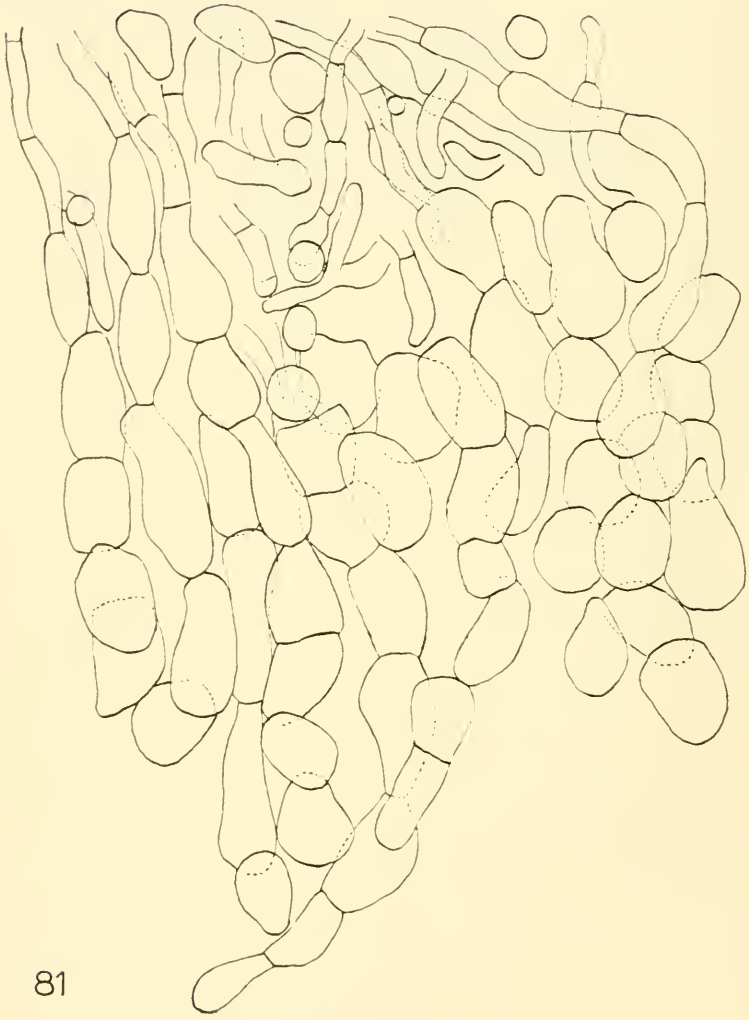
80

Helvella ephippium Lév.

FIG. 79.—Ascospores (Camera lucida drawing, × 700).

FIG. 80.—L. S. through margin of pileus, camera lucida drawing, × 500.

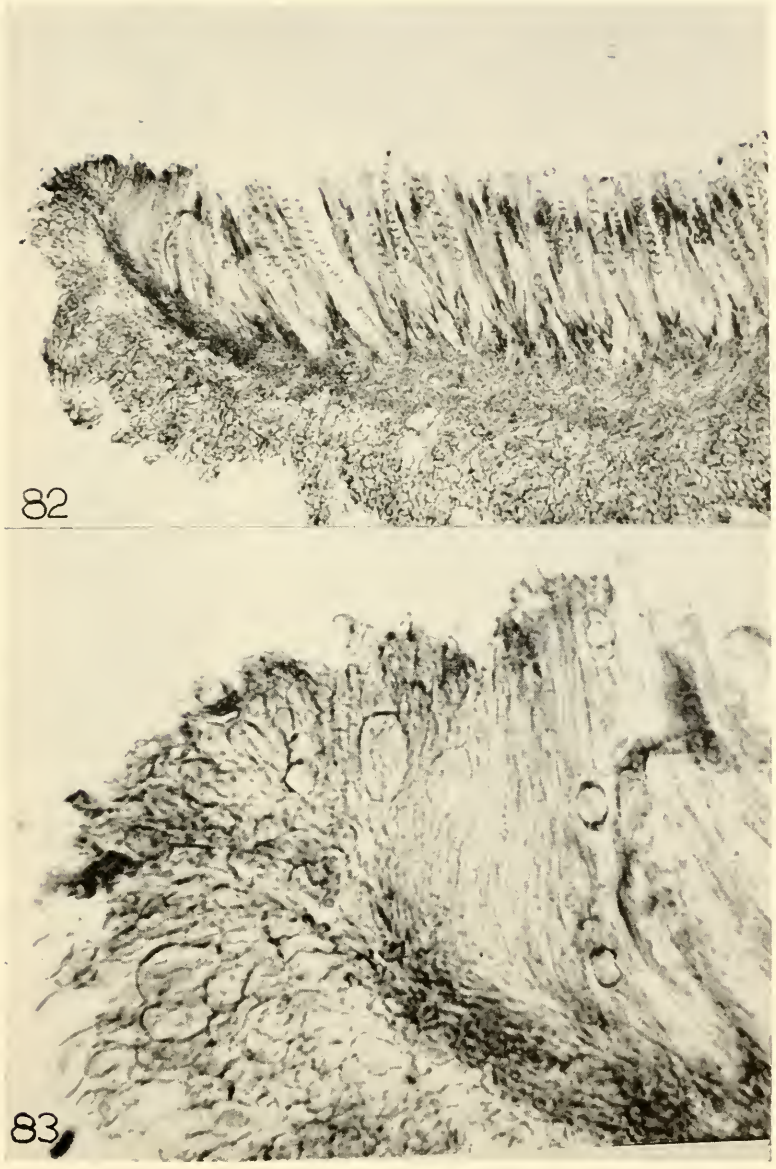
FIGURE 81



Helvella ephippium Lév.

FIG. 81.—L. S. through ectal excipulum and portion of medullary excipulum, camera lucida drawing, × 500.

FIGURES 82, 83



Helvella ephippium Lév.

FIG. 82.—Photomicrograph of L. S. through apothecium showing various tissues, free-hand section, stained with Cotton Blue, × 100.

FIG. 83.—Same section as in Fig. 82, showing marginal excipulum, × 500.

FIGURES 84, 85

Helvella ephippium Lév.

FIG. 84.—Photomicrograph of asci and developing ascospores, free-hand section stained with Phloxine, × 500.

FIG. 85.—Photomicrograph of mature ascospores showing oil globules, × 1000.

FIGURES 84, 85

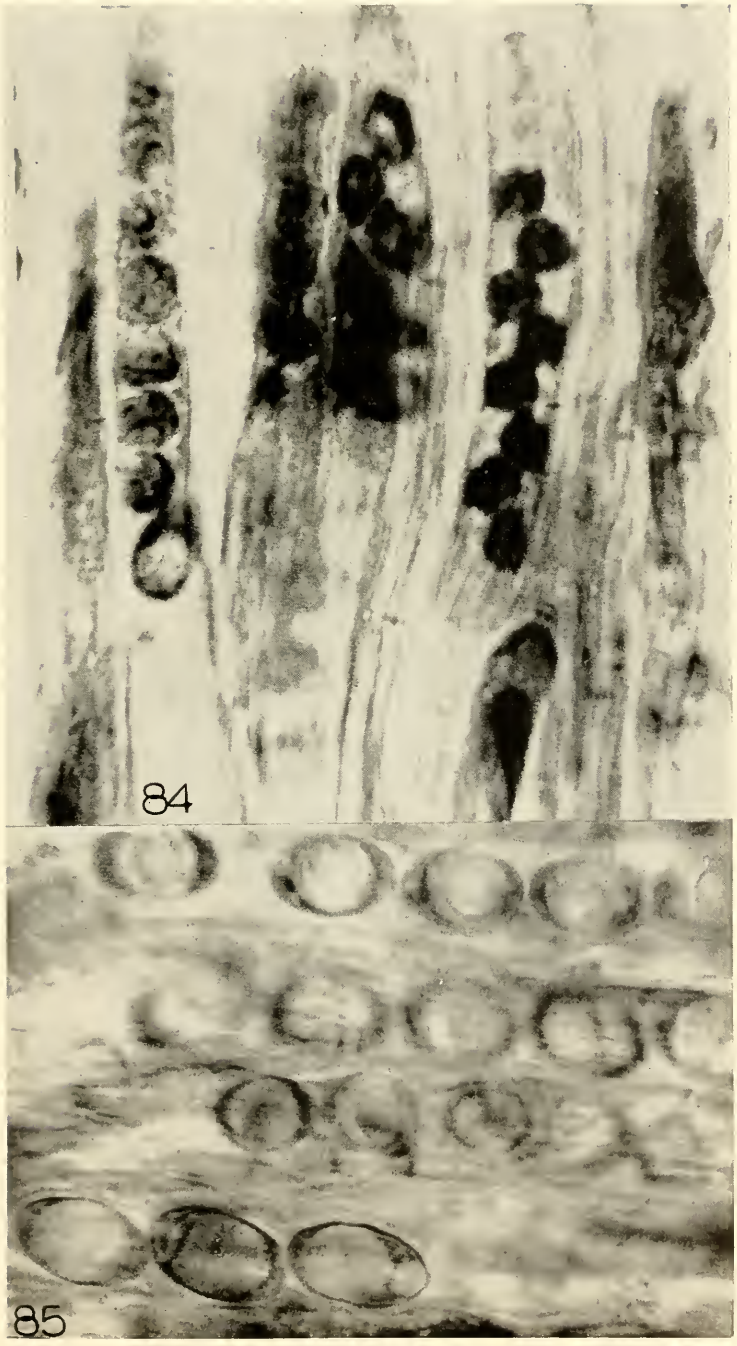


FIGURE 86

Helvella lactea Bond.

FIG. 86.—Apothecia showing variation in form and size (approx. nat. size).

Helvella lacunosa Afzel. *ex* Fr.

Fig. 87.—Apothecia showing variation in form and size (approx. nat. size).

FIGURE 88

Helvella lacunosa Afzel. *ex* Fr.

FIG. 88.—An apothecium from North American form, × 2. Photograph by the courtesy of Department of Plant Pathology, Cornell University.

FIGURE 88

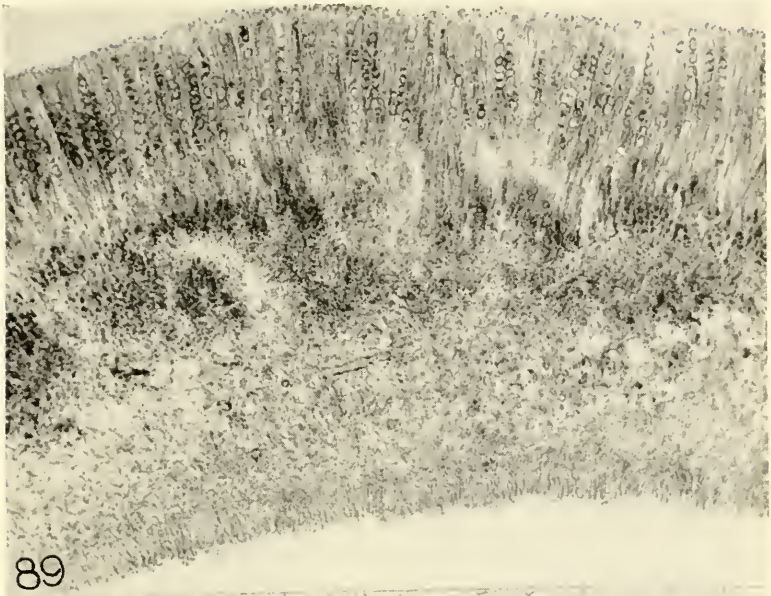
FIGURES 89-90

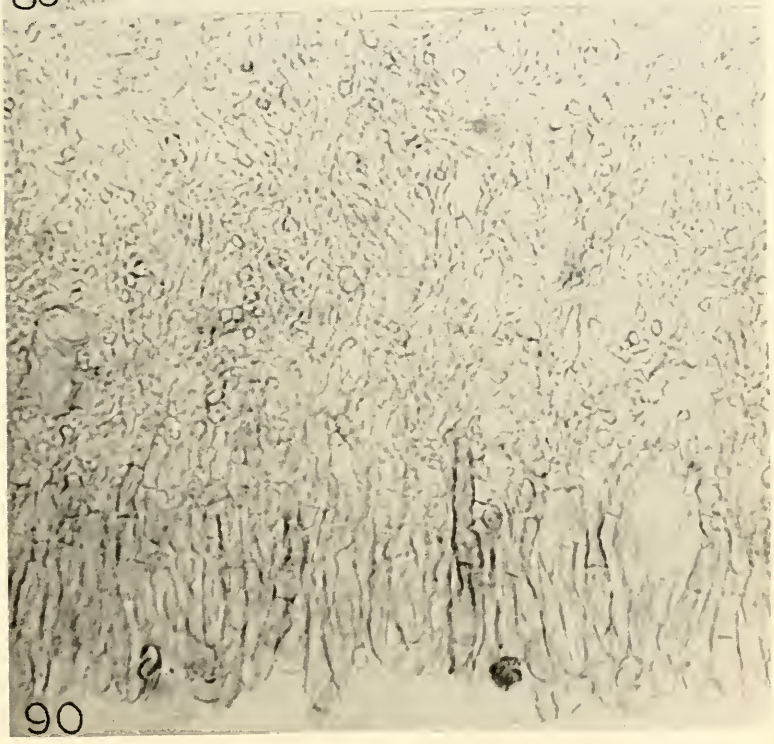
Helvella lacunosa Afzel. *ex* Fr.

FIG. 89.—Photomicrograph of L. S. through middle of an apothecium showing varying tissues, freezing microtome, stained with Cotton Blue, × 100. Material *ex* type *Helvella grisea* Clements which is a synonym of *H. lacunosa.*

FIG. 90.—Photomicrograph of ectal and medullary excipulum, same section as in Fig. 89, × 500.

FIGURES 89-90





FIGURES 91, 92

Helvella lacunosa Afzel. *ex* Fr.

Fig. 91.—Photomicrograph of L. S. through apothecial margin showing ectal excipulum, paraphyses and an ascus, × 500.

Fig. 92.—Photomicrograph of ectal and medullary excipulum, × 500. Material *ex* type *Helvella grisea* Clements.

FIGURES 91, 92

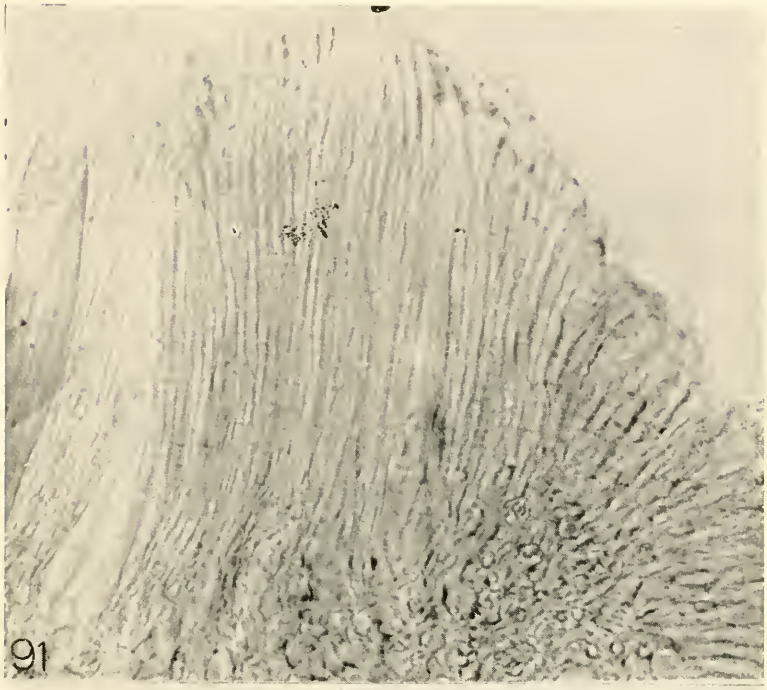
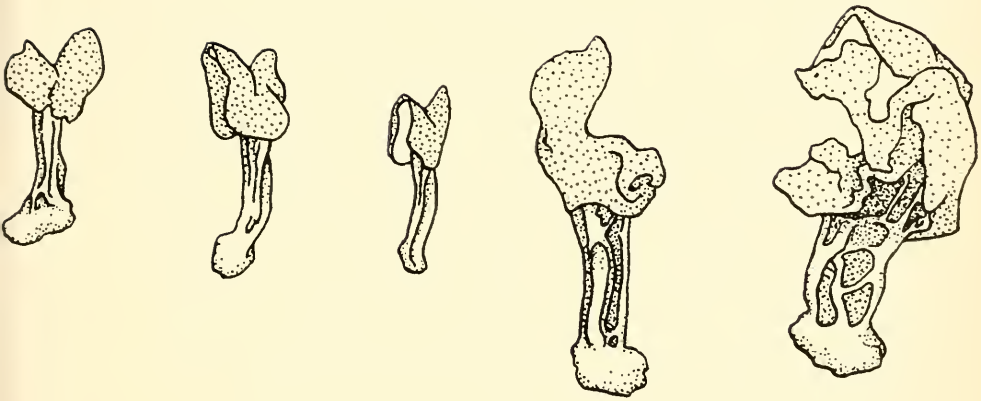


FIGURE 93

Helvella sulcata Afzel. *ex* Fr.

FIG. 93.—Apothecia showing variation in form and size, free-hand drawing from fresh specimens (approx. nat. size).

FIGURE 93



93

FIGURES 94-99 (all camera lucida drawings, × 700)

FIG. 94.—*Helvella acetabulum* (L. *ex* Fr.) Quél., ascospores.

FIG. 95.—*H. atra* König, ascospores.

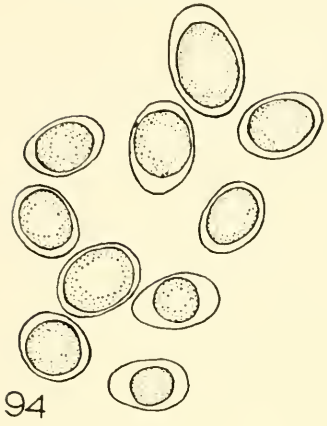
FIG. 96.—*H. calyciformis* Batt. *ex* Quél., ascospores.

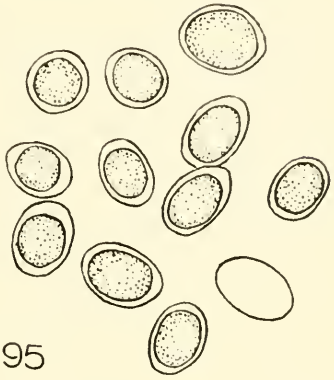
FIG. 97.—*H. crispa* Scop. *ex Fr.*, ascospores.

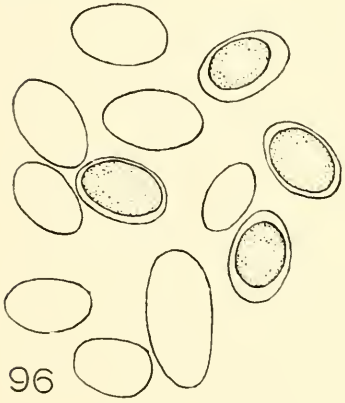
FIG. 98.—*H. elastica* Bull. *ex* Fr., ascospores.

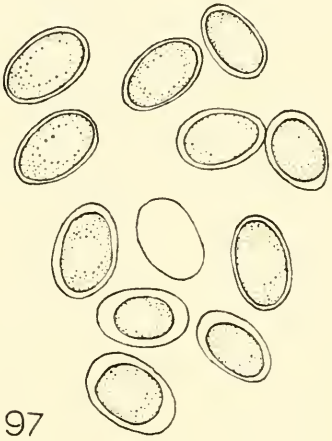
FIG. 99.—*H. lacunosa* Afzel. *ex Fr.*, ascospores.

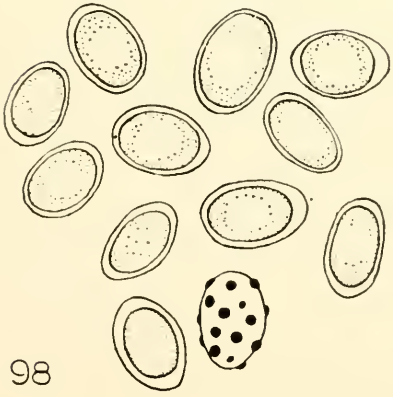
FIGURES 94-99 (all camera lucida drawings, × 700)


94


95


96


97


98

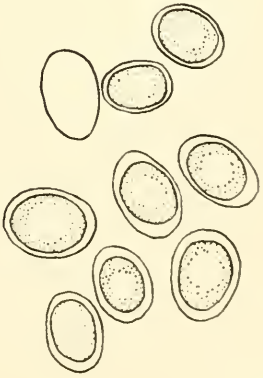

99

FIGURE 100

Morchella angusticeps Peck

FIG. 100.—Ascomata showing general appearance and hymenium ridges (approx. nat. size). Photograph courtesy Department of Plant Pathology, Cornell University.

FIGURE 100

FIGURE 101

Morchella esculenta L. *ex* Fries

FIG. 101.—Ascomata showing variation in shape and size in a single collection near Ithaca, New York (⅓ nat. size).

Morchella esculenta L. *ex* Fries

Fig. 102.—An ascoma showing internal appearance and two ascomata showing external characters (somewhat reduced). Photograph by the courtesy of the Department of Plant Pathology, Cornell University.

FIGURE 103

Ptychoverpa bohemica (Krombh.) Boud.

FIG. 103.—Apothecia showing general appearance (somewhat enlarged). Photograph by the courtesy of the Department of Plant Pathology, Cornell University.

FIGURE 104

Verpa Conica Swartz *ex* Pers.

FIG. 104.—Ascomata showing general appearance (nat. size).

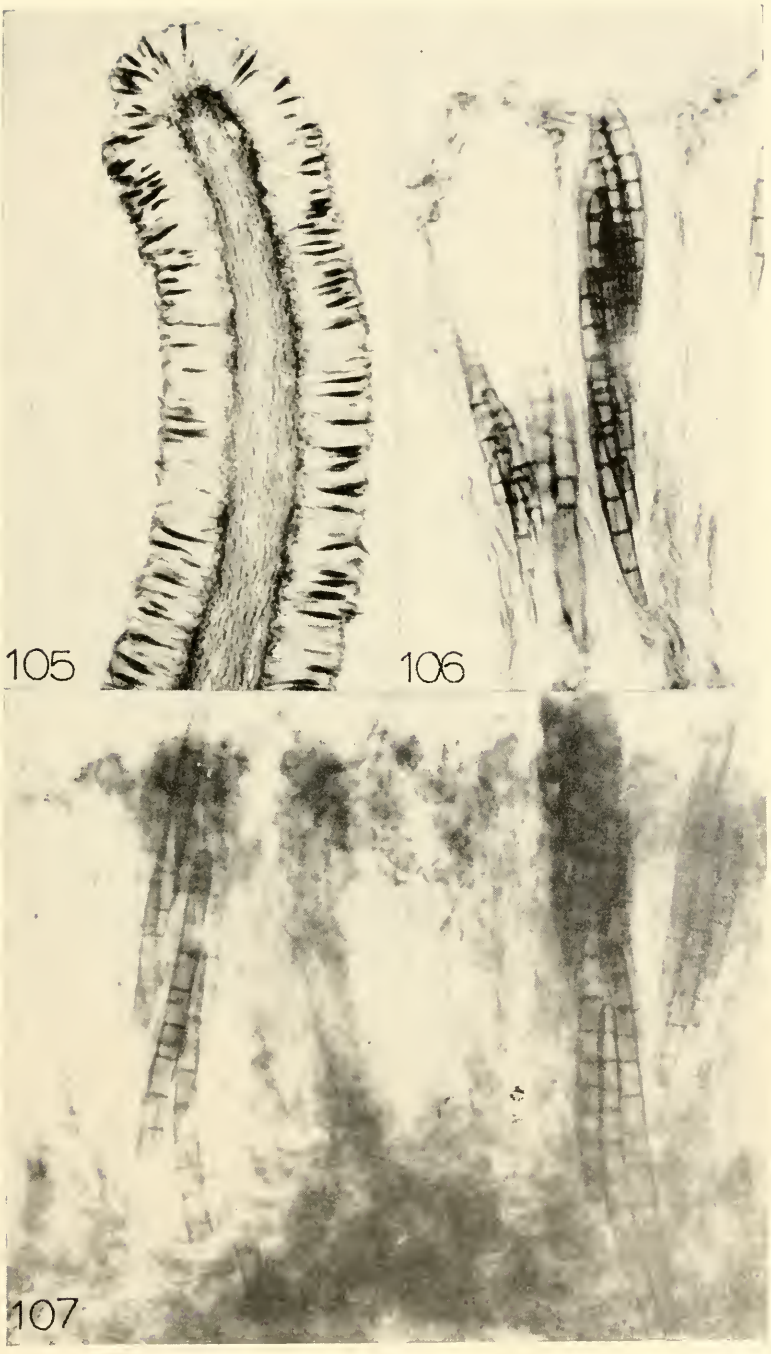
FIGURES 105-107

FIG. 105.—*Geoglossum cohaerens* Durand. Photomicrograph of a median L. S. through a portion of an ascophore, freezing microtome, unstained, × 30.

FIG. 106.—*Geoglossum cohaerens* Durand. Asci, paraphyses and ascospores, unstained, × 500.

FIG. 107.—*Geoglossum* (?) *fallax* Durand, ascospores, unstained, × 500.

FIGURES 105-107



FIGURES 108-112

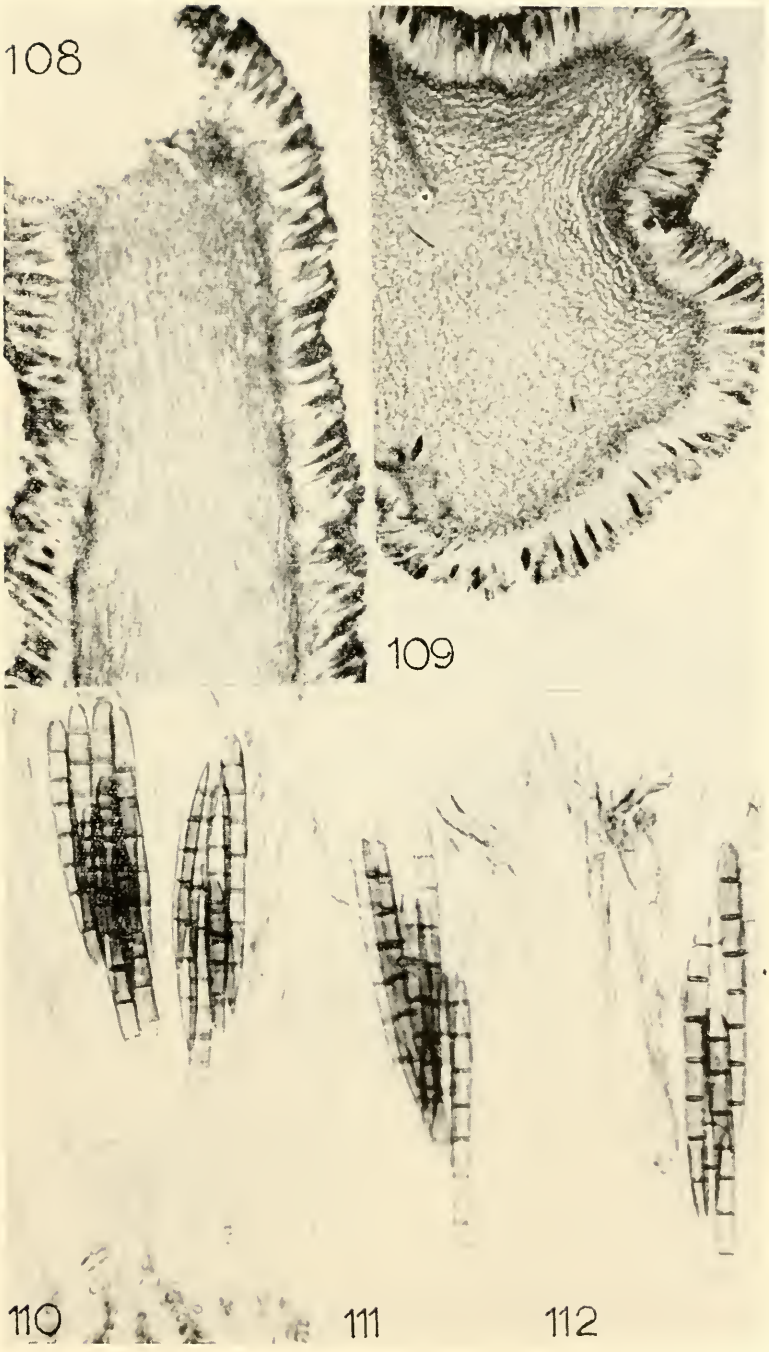
Geoglossum glabrum Pers. *ex* Fr.

FIG. 108.—Photomicrograph of a median L. S. through a portion of an ascoma, unstained, × 30.

FIG. 109.—Photomicrograph of a T. S. through the ascigerous portion of an ascoma, unstained, × 30.

FIGS. 110-112.—Asci, ascospores and paraphyses, unstained, × 500.

FIGURES 108-112



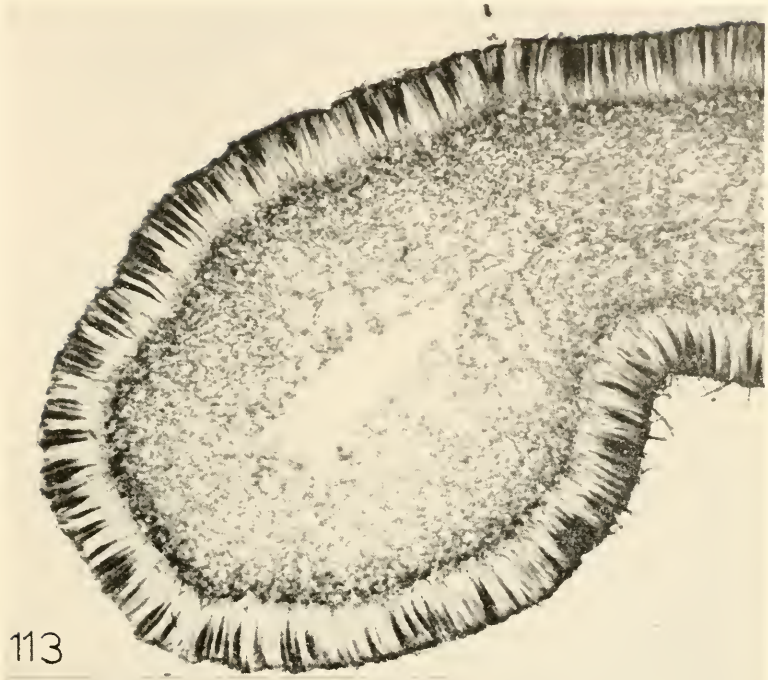
FIGURES 113, 114

Geoglossum japonicum Imai

FIG. 113.—Photomicrograph of a T. S. through the ascigerous portion of an ascoma, unstained, × 30.

FIG 114.—Photomicrograph of asci, paraphyses and ascospores, stained with Cotton Blue, × 500.

FIGURES 113, 114



113

114

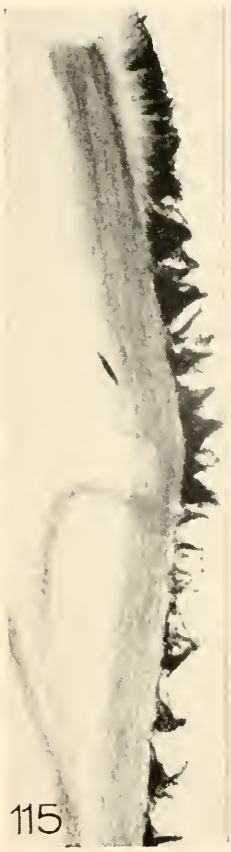
FIGURES 115, 116

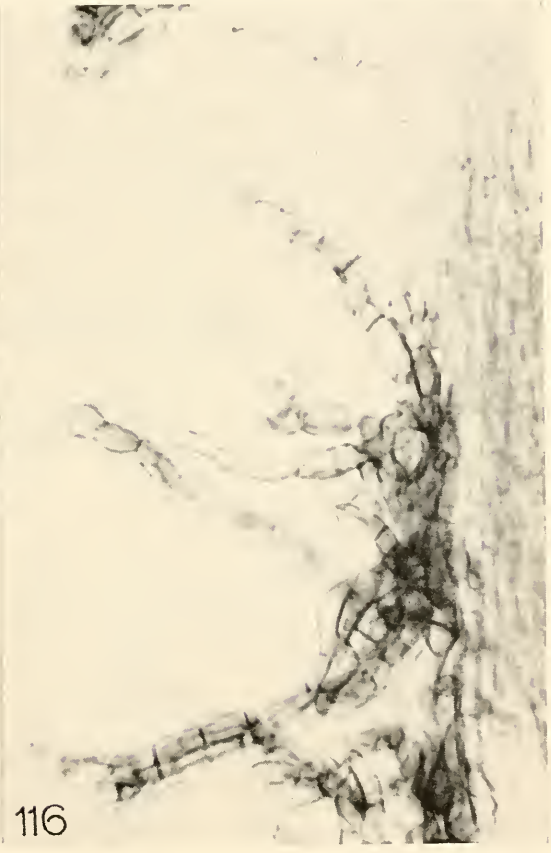
Geoglossum nigritum (Fr.) Cooke

FIG. 115.—Photomicrograph of a median L. S. section through the junction of ascigerous and non-ascigerous portion of ascoma showing paraphyses merging with excipulum of medulla, unstained, × 500.

FIG. 116.—Photomicrograph of a portion of the L. S. of excipulum cells under higher magnification, unstained, × 500.

FIGURES 115, 116



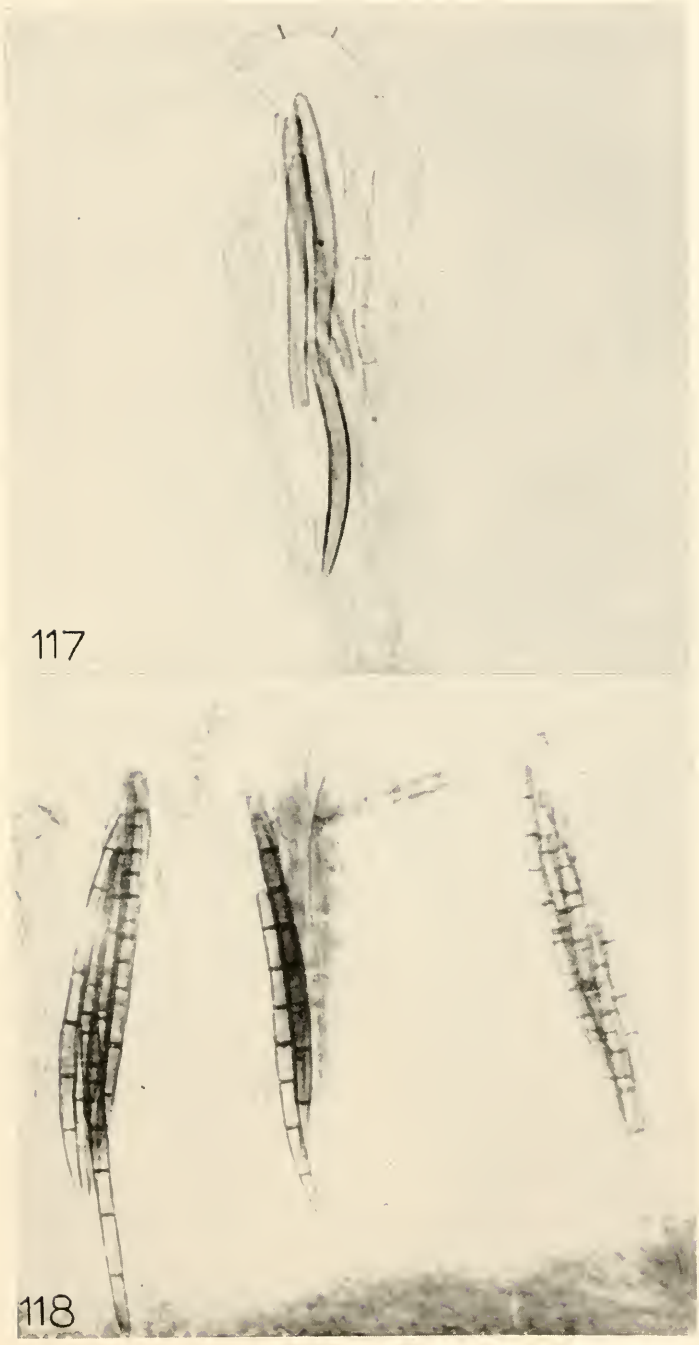


FIGURES 117, 118

Geoglossum nigritum (Fr.) Cooke

FIG. 117.—Asci, paraphyses and young ascospores, unstained, × 500.
FIG. 118.—Mature ascospores and paraphyses, unstained, × 500.

FIGURES 117, 118

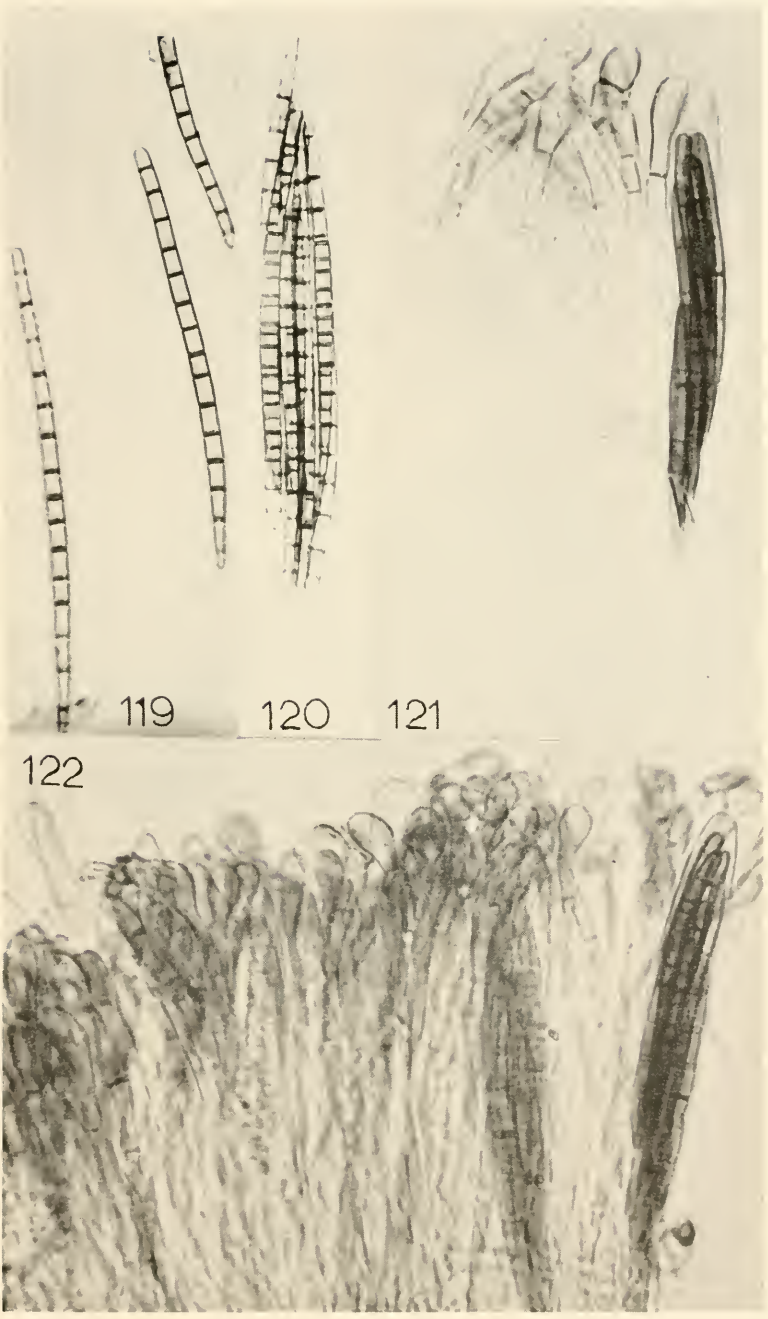


FIGURES 119-122

FIGS. 119, 120.—*Geoglossum pygmeum* Gerard, ascospores, unstained, × 500.

FIGS. 121, 122.—*Geoglossum simile* Peck, ascospores, asci and paraphyses, unstained, × 500.

FIGURES 119-122



FIGURES 123-125

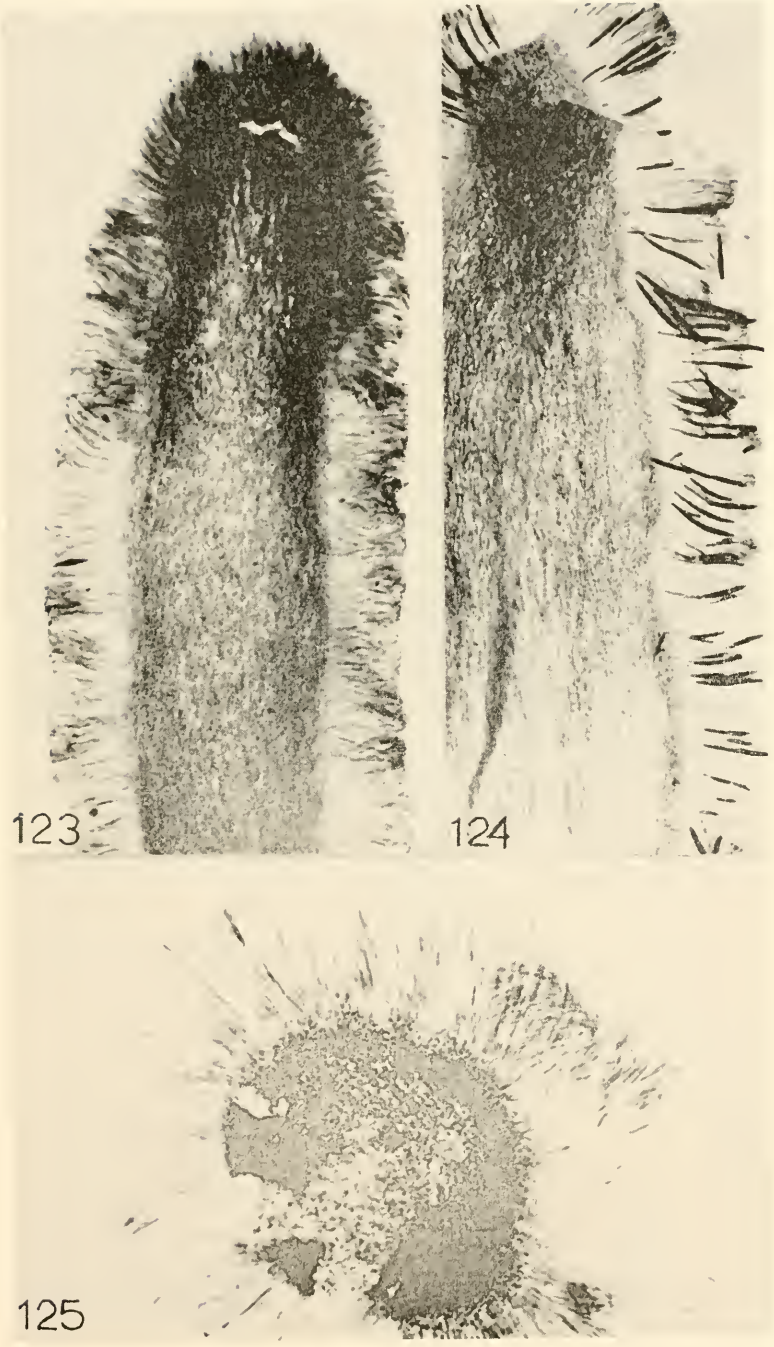
Gleoglossum glutinosum (Pers. *ex* Fr.) Durand

FIG. 123.—Photomicrograph of a median L. S. of young ascigerous portion showing paraphyses and occasional asci. Note the densely colored medulla, unstained, × 30.

FIG. 124.—Photomicrograph of a median L. S. of a mature ascigerous portion. Note the disappearance of pigmentation from medulla, unstained, × 30.

FIG. 125.—Photomicrograph of a T. S. of young ascigerous portion showing medulla, paraphyses and occasional pieces of asci, unstained, × 30.

FIGURES 123-125



FIGURES 126-128

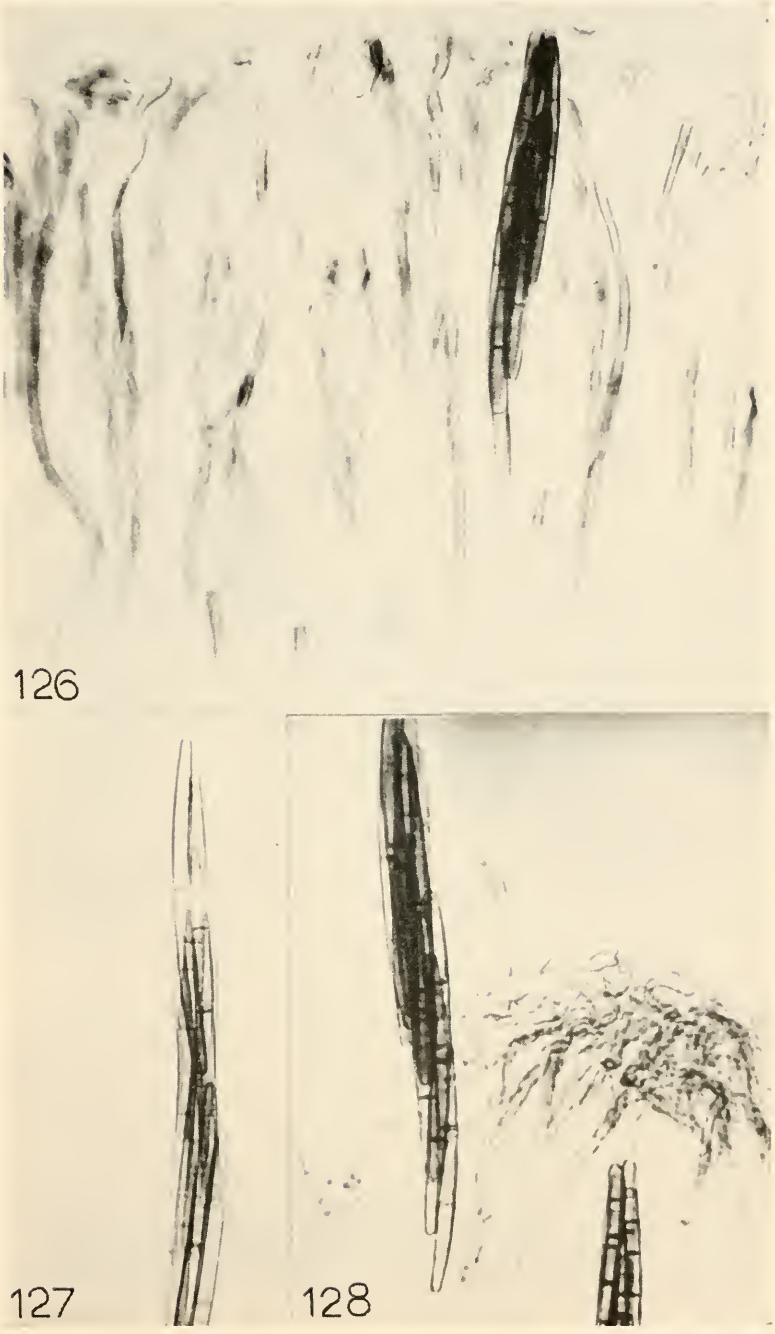
Gleoglossum glutinosum (Pers. *ex* Fr.) Durand

FIG. 126.—Photomicrograph of paraphyses, an ascus and young ascospores, unstained, × 500.

FIG. 127.—Photomicrograph of ascospores, unstained, × 500.

FIG. 128.—Photomicrograph of paraphyses and an ascus with ascopores, unstained, × 500.

FIGURES 126-128



FIGURES 129-132

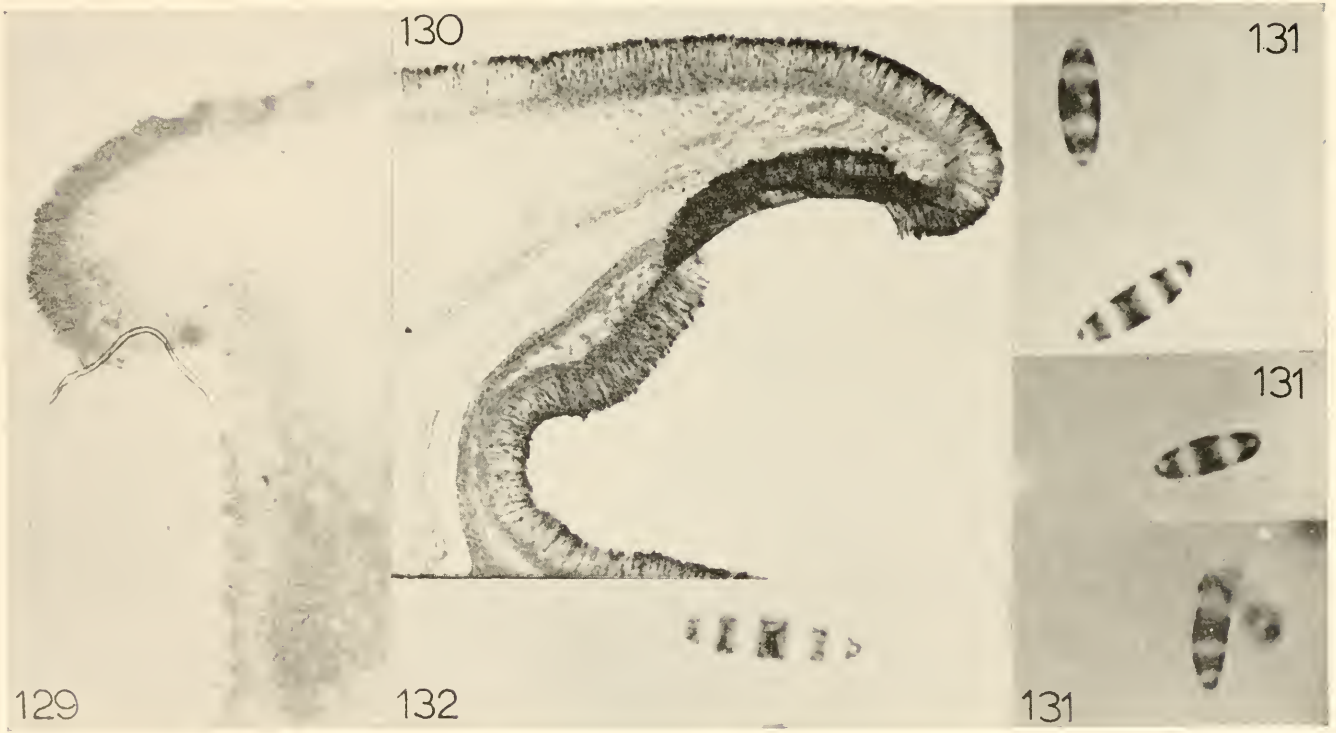
Leotia lubrica Scop. *ex* Fr.

FIG. 129.—Photomicrograph of a median L. S. through a young apothecium, stained with Cotton Blue, × 30.

FIG. 130.—Photomicrograph of a median L. S. through a mature pileus showing various tissues, stained, × 30.

FIG. 131.—Ascospores stained with Cotton Blue or Phloxine. Note the cross-bands of cytoplasm which falsely resemble septa in unstained preparation, × 100.

FIG. 132.—An ascospore with five cross-bands, stained in Phloxine, × 1000.


130
131
131
129
132
131

FIGURES 133, 134

Mitrula sp.

FIG. 133.—An ascus and paraphyses. Note cross-bands in spores similar to that of *Leotia* spp., stained with Phloxine, × 500.

FIG. 134.—Two asci arising together from croziers, stained with Phloxine × 500.

FIGURES 133, 134

FIGURES 135-137

Trichoglossum octopartitum Mains

FIG. 135.—Photomicrograph of a median L. S. through ascigerous portion showing medulla, subhymenium, hymenium and deep-seated setae, unstained, × 30.

FIG. 136.—Photomicrograph of asci, ascospores and setae, unstained, × 500.

FIG. 137.—Photomicrograph of a T. S. through ascigerous portion showing asci, paraphyses and deep-seated setae, unstained, × 100.

FIGURES 135-137

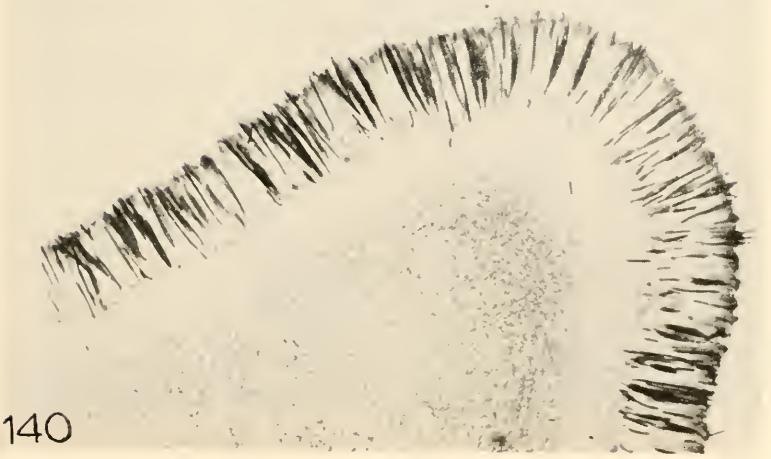
FIGURES 138-140

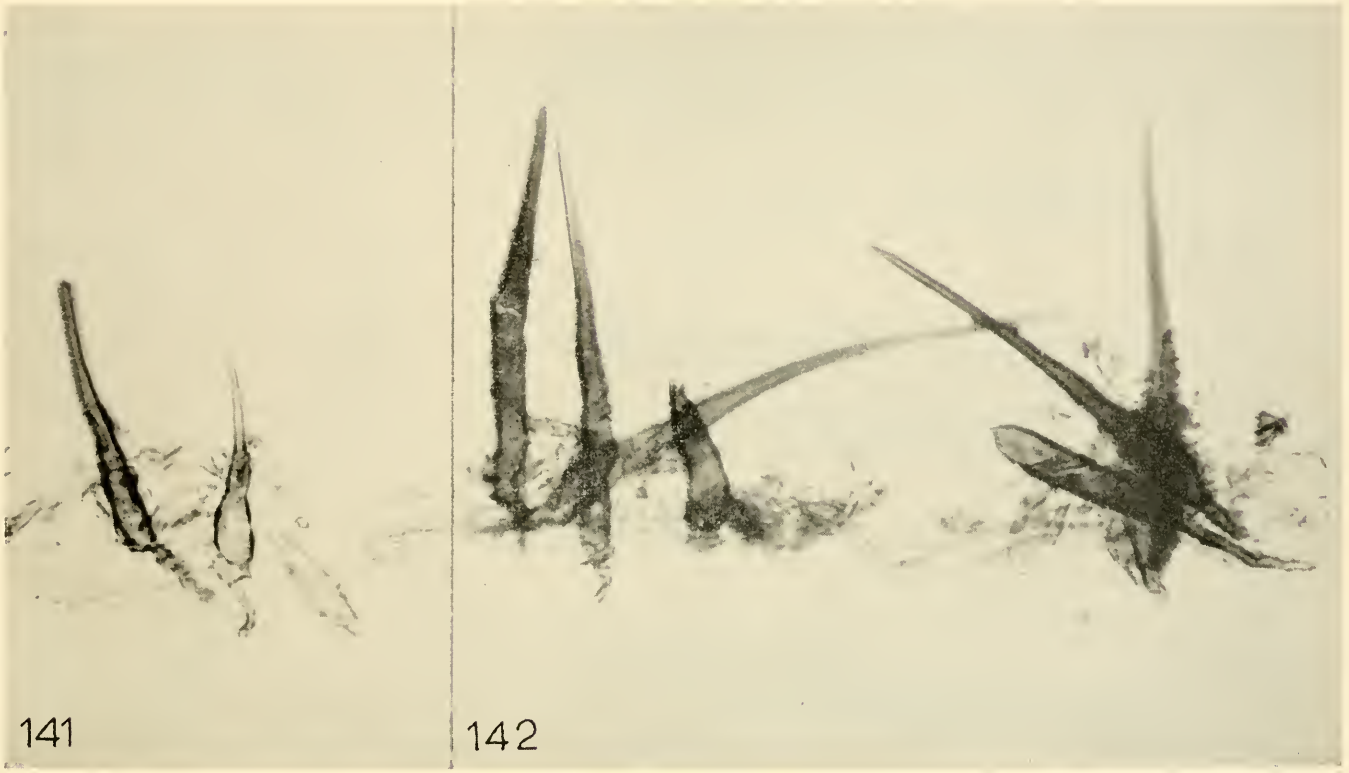
FIG. 138.—*Trichoglossum octopartitum* Mains, photomicrograph of two asci stained with iodine showing their distinct pores and young ascospores, × 500.

FIG. 139.—*Trichoglossum hirsutum* (Pers. *ex* Fr.) Boud., photomicrograph of asci, setae and ascospores, unstained, × 500.

FIG. 140.—*Trichoglossum hirsutum* (Pers. *ex* Fr.) Boud., photomicrograph of T. S. of ascigerous portion showing various tissues, unstained, × 30.

FIGURES 138-140





Trichoglossum hirsutum (Pers. *ex* Fr.) Boud.

FIGS. 141, 142.—Photomicrographs of hairs arising from hyphal ends in medulla on stipe, unstained, × 500.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

VOL. XLIV] SEPTEMBER 13, 1963 [No. 7

New Ceratinini from Australia (Hymenoptera, Apoidea) [1]

BY

CHARLES D. MICHENER [2]

The following descriptions are published at this time, in advance of a larger work on the systematics of Australian bees, in order to make the names available for papers on the behavior and larval structure of the species concerned.

Exoneurella new genus.

Type species: *Exoneura lawsoni* Rayment, 1946.

This genus is erected to contain a small black species similar in appearance to a small species of *Exoneura*. The genus is related to *Exoneura* as shown by the body form, the soft shining integument, the shape of the clypeus, and agrees with *Exoneura* also in the following features: Mandibles tridentate in female, rounded edentate in male; maxillary palpi five segmented; wings with venation as in *Exoneura* except as described below; graduli of second to fourth sterna faint, weakly recurved medially; genitalia of male with stylus reduced, broader than long, probably immovable, penis valve large, armed with long anteriorly directed bristles on outer surface.

Exoneurella most closely resembles such small species of *Exoneura* as *E. ploratula* Cockerell and *gracilis* Cockerell. It agrees with such species not only in size but in the following features which are group characters within the genus *Exoneura*: Clypeus closely approaching antennal bases so that clypeoantennal distance is in both sexes (especially male) less than diameter of antennal

1. Contribution number 1153 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

2. It is a pleasure to acknowledge facilities provided by the University of Queensland through the courtesy of Mr. F. A. Perkins, Reader in Entomology and head of the Department of Entomology of that Institution. Studies in Australia were possible thanks to a research grant from the Fulbright program of the United States Government. Subsequent systematic studies were facilitated by a grant from the National Science Foundation.

10—3961

socket; scape not reaching anterior ocellus; head and thorax of male not covered with long dense hairs; eyes of male not dilated, separated by distance greater than ocular width; fore tarsi of male of ordinary form, not attenuate, first two segments taken together slightly shorter than tibia; hind basitarsus of male shorter than tibia, about half as wide as tibia, parallel sided; vein Cu_1 represented by a short stub, ending abruptly, and not or scarcely continued as a brownish line; pterostigma large and broad, as long as costal margin of marginal cell.

The following are the distinctive features of the genus which separate it from all species of *Exoneura*: Second submarginal cell narrowed toward costal margin which is short, often less than half as long as first transverse cubital vein; basitibial plate not defined; sixth tergum of female distinctly concave dorsally, profile distinctly concave, apex produced to median, bidentate, upturned projection which is not at all hidden by hair as is the far smaller median projection of *Exoneura*.

In addition to the characters of the adults, *Exoneurella* differs from *Exoneura* in striking features of the larva. Larvae of *Exoneurella* lack ventrolateral projections on the body segments which occur in *Exoneura* and have large ventroposterior hairy projections on the sides of the head which are absent in *Exoneura*. The details of the larval structure will be described and illustrated by Syed (1962).

The immature stages of *Exoneurella* live together in a hollowed pithy stem as in *Exoneura* and not in separate cells as in *Ceratina*. The individual females are solitary, not forming associations of several adult females in a single nest such as occur in *Exoneura* and *Allodapula*.

Exoneurella lawsoni (Rayment)

Exoneura lawsoni Rayment, 1946, Victorian Naturalist, 62: 230 (male, not female or larva).

Rayment included material from more than one nest and evidently of two species in his description of *lawsoni*. The male is the most fully described sex and the labeled type in the collection of the Commonwealth Scientific and Industrial Research Organization in Canberra is a male. Therefore the specific name should be applied to the male. The larvae and presumably the female described by Rayment belong to a species of *Exoneura*. The parallel inner orbits and the lack of pale yellow at the bases of the tibiae

are among the characters of the female attributed to *lawsoni* by Rayment which do not agree with my females of *lawsoni*.

Female: Length 5.0 to 5.75 mm. *Color:* Shining black, with cream-colored mark on clypeus extending from upper nearly to lower margin, sides nearly parallel except that at upper end pale mark abruptly expands to full width of clypeus so that mark is T-shaped. Posterior pronotal lobe, costal sclerite of wing base, and small spots at apices of femora and bases of tibiae cream colored. Labrum and antenna (especially under surface of flagellum) brownish; anterior tibia and tarsus yellowish brown; middle and hind basitarsi grayish brown; other tarsal segments brown; tegula translucent brown. *Pubescence:* Short, sparse, grayish white, scopa similar to that of *Exoneura*, hairs of dorsum of fourth tergum longer than those of other terga and slightly spiculate so that they appear thick. *Structure:* Relative head measurements as follows: width 19.5; length 17.5; lower interocular distance 9.5; upper interocular distance 13; clypeal length 8. Genal area in side view rounded posteriorly, about three-fourths as wide as eye seen in same view; basitarsi shorter than corresponding tibiae, first two tarsal segments equal in length to anterior tibia, longer than middle and hind tibiae. *Punctation:* Clypeus with punctures, surface minutely roughened; rest of face impunctate or nearly so; mesoscutum impunctate except for extreme margins which are minutely roughened or finely punctate; scutellum distinctly punctured, metanotum and dorsal surface of propodeum dull, roughened, rest of thorax impunctate except for minute piliferous punctures; metasoma with surface minutely roughened, that of last three terga almost dull; first three terga with scattered rather coarse punctures; last three terga with coarser and closer punctures.

Male: Length 4 mm. Similar to female. Differing from description as follows: Entire clypeus, small lateral face marks next to broad part of clypeus (sometimes extending upward to above level of tentorial pits), most of labrum, small subapical mandibular area, and under surface of scape pale yellow; tarsi testaceous, middle and hind basitarsi dull whitish. Hairs of fourth tergum not longer than those of others. Shape of clypeus and face about as in female, eyes more strongly converging below so that antennocular and upper clypeocular distances are only about equal to width of scape; genal area less than half as wide as eye seen from side.

Localities: Deepwater, New South Wales; four miles south of

Warwick, Stanthorpe, and Kilcoy, Queensland. Dates of activity will be given in a forthcoming paper on the habits of this species.

Some of the females from Warwick and Kilcoy have the lateral margins of the sixth tergum of the female a little more produced, shoulder like, than in specimens from the highlands of New South Wales and southernmost Queensland.

All specimens were from nests, mostly in dead stems of *Verbena bonarensis* and other weeds.

Exoneura obscuripes new species

This is a large *Exoneura* similar to *E. hamulata* Cockerell, *bicolor* Smith, etc., which species it resembles in the broad head with the inner orbits subparallel. It differs from the above-mentioned species in having dark brown or black legs with brown to black hair on them and in the largely black first three metasomal terga. The dark coloration is like that of *E. baculifera* Cockerell, which, however, is a somewhat smaller bee with the inner orbits distinctly converging below. The species of *Exoneura* are often very similar in adult characters. The larva of *obscuripes* will be described by Syed (1962).

FEMALE: Length nearly 8 mm. *Color:* Head and thorax black; underside of flagellum brown; underside of scape, median mandibular area, and part of labrum dark red brown; legs dark brown (black in some paratypes); tegula dark tranluscent brown; clypeus with pale yellow mark extending full length of clypeus, narrowest near apical margin, upper end extending full width (or nearly so) of clypeus, not or little hooked downward at dorsolateral angles, therefore reaching (or nearly reaching) upper lateral clypeal margins but not extending down along them for any great distance; margins of yellow area in most specimens not sharply defined. Metasoma dark red, first and second terga black (sometimes with apical margins red, second sometimes with basolateral or apicolateral red patches); third tergum with broad transverse median black band. *Pubescence:* Short and sparse, that of head black, on underside fuscous or in certain lights reddish; that of thorax fuscous or gray, somewhat reddish beneath; that of legs grayish, yellowish on upper surfaces and yellowish red on under surfaces of fore and middle tarsi; scopa of hind tibia and basitarsus (and sometimes hairs of outer side of middle basitarsus) black, appearing reddish in some lights (dark reddish brown in some paratypes); metasoma with tergal pubescence black, sternal pubescence dull whitish.

Structure: Relative head measurements as follows: width 12.2, length 10; lower interocular distance 6.8; upper interocular distance 7.5; clypeal length 4.6. Genal area in side view rounded posteriorly, slightly wider than eye seen in same view; front and hind basitarsi slightly shorter than corresponding tibiae, middle basitarsus longer; vein Cu_1 gradually tapering, not a short stub. *Punctation:* Not different from that of *E. hamulata.*

Holotype Female: Binna Burra, near Lamington National Park, McPherson Range, southern Queensland, December 8, 1958, in nest number 292 (C. D. Michener). Four paratype females: same data, but from nests numbered 277 and 290. Four paratype females, same locality, January 11, 1959, from nests numbered 457 and 458 (Mary H. Michener).

The holotype will be deposited in the collection of the Commonwealth Scientific and Industrial Research Organization, Canberra; paratypes will be placed in the Snow Entomological Museum, University of Kansas, and the British Museum (Natural History).

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Comparative Studies of Larvae of Australian Ceratinine Bees (Hymenoptera, Apoidea)[1]

BY

ISHFAQ HUSSAIN SYED[2]

INTRODUCTION

The purposes of this work are to shed light on the finer details of structure of Australian ceratinine bee larvae of the genera *Exoneura*, *Inquilina* and *Exoneurella*, to compare these with larvae of *Allodapula* described elsewhere (Michener and Syed, 1962) and to interpret insofar as possible the number of larval stages in some of the species of these genera.

The following two paragraphs by Dr. Charles D. Michener provide an evolutionary and functional orientation for this morphological investigation:

"The larvae of the genera listed above (with those of their relative, *Allodape*, of Africa) are no doubt the most extraordinary bee larvae in the world. Their peculiar features are doubtless associated with the unusual biology of these bees, which rear their larvae (by progressive feeding) together in a common burrow in wood or pith with no separate cells. The larvae are therefore in contact with a more diversified and active environment than other bee larvae, most of which develop in closed, mass provisioned cells. The larvae have undergone a considerable evolutionary radiation in adjustment to this situation and have evolved various projections which presumably replace the appendages which have been reduced or lost in larvae of all Clistogastra. This radiation appears to have been partly independent of the evolution of adult characters.

1. Contribution number 1154 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

2. I am greatly indebted to Dr. Charles D. Michener of the Department of Entomology, The University of Kansas, Lawrence, Kansas, for his guidance in the preparation of this paper. My thanks are also due to the U. S. Educational Foundation in Pakistan and the Institute of International Education which awarded me a Fulbright Smith-Mundt Scholarship for the academic year 1960-61.

"The peculiarities of the larvae include (1) hairyness (probably having protective and tactile importance); (2) the middorsal tubercle of the first abdominal segment and the long apex of the abdomen (for locomotion or maintaining position in the nest, *Allodapula*); (3) the medially hinged body (probably with the same function, *Exoneurella*); (4) the long and sometimes branched arms or exaggerated ventrolateral tubercles (*Exoneura, Inquilina*), the large inferior lateral lobes of the head (*Exoneurella*), and the long hairs on the lateral prolongations of the head (*Allodapula*), all of which probably function to hold or manipulate the food mass which is held on the venter of the larva; and (5) the long and sometimes modified antennae (all except *Allodapula,* but especially *Exoneurella*) and the median frontal projection (some *Exoneura*) which probably serve as tactile organs."

Larvae of several species of Australian *Allodapula* were described by Michener and Syed (1962). Larvae of numerous species of *Exoneura* were described by Rayment (1946a, b, c; 1948; 1949a, b; 1951, 1954) and Erickson and Rayment (1951). Unfortunately few of the finer details of larval structure were described or illustrated in those papers. The larva of the genus *Exoneurella* is here described for the first time. It is quite probable also that the larva of *Inquilina* is described here for the first time. Rayment describes some larvae (under the generic name *Exoneura*) which he attributed to species which fall in the genus *Inquilina.* However, species of that genus are social parasites often associated with larvae of their hosts and the identity of larvae in nests with them is therefore in doubt.

MATERIAL AND TECHNIQUE

The material was collected by Dr. Charles D. Michener in New South Wales and southern Queensland in 1958-59 (Table 1). The material was preserved by dropping live larvae into Dietrich's (Kahle's) solution in the field. The material was excellently preserved; even the ventrolateral tubercles were fully expanded. For most species the studies were based on mature larvae because of nonavailability of larvae of younger stages; however, for *Exoneura variabilis* Rayment, *Exoneura hamulata* Cockerell and *Exoneurella lawsoni* (Rayment) an attempt has been made to determine the number of larval stages. These estimates were made on the basis of measurements of heads of larvae and are supported by other characters such as the presence or absence of ventrolateral tubercles and numbers of setae. Even for these species the number of smaller

TABLE I.—Species Studied and Sources of Material

SPECIES	Number of larvae	Localities	Dates
E. variabilis	60 mature 105 younger	Tamborine Mt., Binna Burra (Lamington National Park), Cunningham's Gap; all in Queensland.	Oct., Dec., 1958; Jan., Feb., Mar., 1959.
E. hamulata	13 mature 14 younger	Tibrogargen (near Beerwah), Queensland.	Oct., 1958; Jan., Feb., 1959.
E. concinula	4 mature	Roseville, New South Wales.	Jan., 1959.
E. obscuripes	7 mature	Binna Burra (Lamington National Park), Queensland.	Dec., 1958.
E. sub-baculifera	1 mature 2 younger	Cunningham's Gap., Queensland.	Nov., 1958.
I. excavata	4 mature 3 small	Binna Burra (Lamington National Park), Tamborine Mt., both in Queensland.	Dec., 1958; Jan., 1959.
E. lawsoni	58 mature 105 younger	Warwick, Moore, Stanthorpe, all in Queensland; Tenterfield, New South Wales.	Sept., Oct., Nov., Dec., 1958; Mar., 1959.

larvae was not sufficient to make determination of number of stages positive.

Illustrations of whole larvae were made in lateral view using an eye-piece grid and graph paper.

Illustrations of heads were prepared from a study of whole heads both before and after clearing in caustic.

In order to study the mandibles in detail they were removed from the head and sometimes cleared with caustic or the whole head was treated in the same manner. Orientation for illustration was by means of mandibular apodemes and articulations. In the inner view the adductor apodeme is as nearly as possible directly above the adductor, while in the ventral view the points of articulation are one above the other and the apodemes at the lateral extremities of the mandibular base. This is the same system as that used by Michener (1953).

Spiracles were studied either by removing them with bits of adjoining integument and clearing them in caustic or usually by clearing decapitated larvae. The spiracles were examined without staining on temporary slides in water at magnification up to 396 ×.

Lateral views of spiracles are optical sections while facial views show structures visible at all levels.

For preservation, the mandibles, heads or other detached parts such as spiracles were placed in alcohol in small vials within the large vials containing the larvae.

MORPHOLOGICAL AND SYSTEMATIC ACCOUNTS

General group characters

These ceratinine bee larvae possess certain group characters which have been listed by Michener and Syed (1962) as follows: 1. Dorsolateral tubercles absent. 2. Head rather weakly sclerotized. 3. Anterior and posterior tentorial pits, epistomal suture and cleavage line inconspicuous. 4. Labroclypeal suture distinct except in *Exoneurella*. 5. Salivary opening not seen and presumably absent.[3] 6. Spiracle with peritreme, collar around primary tracheal opening also present; atrium not projecting above body surface.

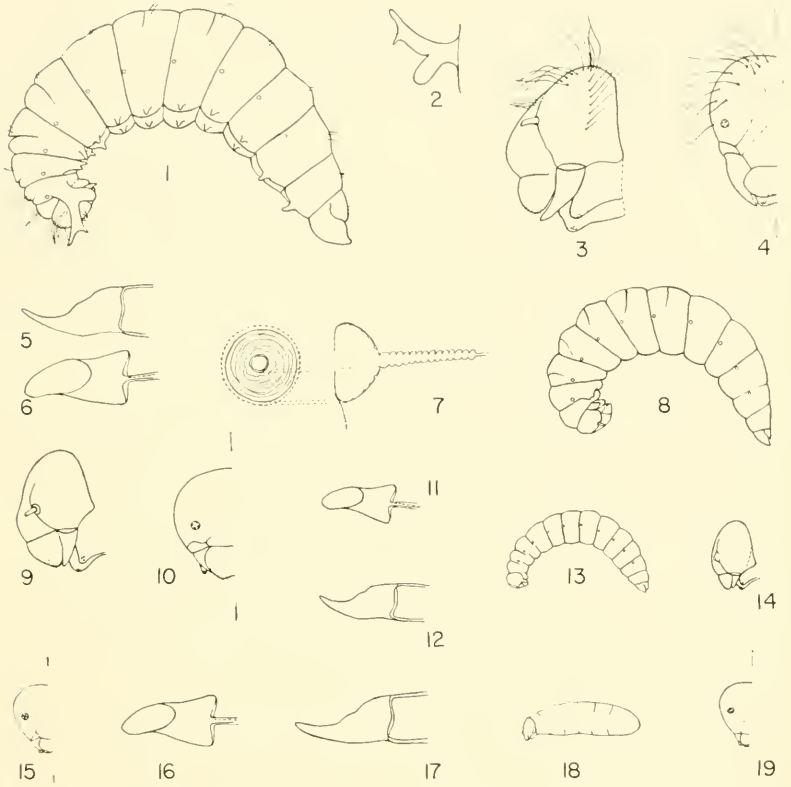
Exoneura variabilis Rayment

Mature larva (Fig. 1): Slender with intersegmental lines distinct and with additional transverse furrows in some segments. Dorsal elevation of each segment not distinct except for those of seventh, eighth and ninth abdominal segments. Ventrolateral tubercles conspicuous and forming two distinct rows on each side of body except on meso- and metathoracic segments, each of which has one large ventrolateral tubercle; prothoracic and last abdominal segments without ventrolateral tubercles; ventrolateral tubercles of abdominal segments somewhat conical and pointed at tips; ventrolateral tubercle of mesothorax (Fig. 2) very large and with two distinct lobes, anterior lobe further bifid, each division with a pointed tip, posterior lobe somewhat globular and rounded at tip; ventrolateral tubercle of metathorax larger than abdominal ventrolateral tubercles but considerably smaller than mesothoracic tubercle and distally bifid. Body with short setae present only on dorsal aspects of segments, lateral and ventrolateral parts hairless.

Head (Figs. 3, 4) somewhat spherical in shape, laterally not produced, width 0.70-0.80 mm. Small setae present mostly laterally and frontolaterally. Antenna well-developed, elongate and tapering distally and with a broad base, four to five sensory papillae present at tip. Labrum somewhat subtruncate apically with a small depression in middle region and with several small papillae mostly towards

3. For a note on the "salivary opening" illustrated for *Ceratina*, see Michener and Syed (1962).

apical region. Maxillary and labial palpi small but distinct, former with three and the latter with two sensory papillae. Mandible (Figs. 5, 6) broadly rounded apically and with a somewhat spoon-shaped concavity; upper and lower margins toothless.



FIGURES 1-19.—*Exoneura variabilis*. 1. Mature larvae. 2. Lateral view of expanded mesothoracic ventrolateral tubercle of same. 3, 4. Lateral and frontal views of head of same. 5, 6. Inner and ventral views of mandible of same. 7. Spiracle of same. 8. Third-stage larva. 9, 10. Lateral and frontal views of head of same. 11, 12. Inner and ventral views of mandible of same. 13. Probable second-stage larva. 14, 15. Lateral and frontal views of head of same. 16, 17. Inner and ventral views of mandible of same. 18. Probable first-stage larva. 19. Frontal view of head of same.

Spiracular atrium (Fig. 7) with a few feeble ridges towards periphery and without spines, ridges near atrial opening with small projections.

Larva (Fig. 8) of third stage or a stage next to mature larva: Similar to description of mature larva but smaller. Ventrolateral tubercle of mesothorax represented by small bifid protuberance;

ventrolateral tubercles absent on all other body segments. Body hairless.

Head (Figs. 9, 10) including mandibles (Figs. 11, 12) similar to that of mature larva but small in size, width 0.56-0.60 mm. Setae absent.

Larva (Fig. 13) probably of second stage: Similar to description of mature larva but considerably smaller. Intersegmental lines not complete in thoracic region. Ventrolateral tubercles absent. Body hairless.

Head (Figs. 14, 15) including mandibles (Figs. 16, 17) similar to that of mature larva but smaller in size, width 0.36-0.45 mm. Antenna represented by a high prominence provided with five sensory papillae. Setae absent.

Larva (Fig. 18) probably of first stage: Very different from mature larva, very small in size, without intersegmental lines. Ventrolateral tubercles absent. Body hairless.

Head (Fig. 19) similar to that of mature larva but smaller in size, width 0.30-0.33 mm. Antenna represented by low prominence provided with four sensory papillae. Labroclypeal suture not distinct.

Rayment's types of *E. variabilis* are teneral so that the identification is subject to a slight element of doubt.

Exoneura hamulata Cockerell

Mature larva (Fig. 20): Robust, with distinct intersegmental lines and with additional transverse furrows particularly in thoracic region. Dorsal elevations of abdominal segments more conspicuous than in *E. variabilis.* Ventrolateral tubercles conspicuous, in two rows on each side of body except on mesothoracic and metathoracic segments where there is one row on each side; prothorax and last abdominal segment without ventrolateral tubercles; ventrolateral tubercles of abdominal segments as in *E. variabilis,* somewhat conical and pointed at apices, but larger in size than in *E. variabilis;* mesothoracic ventrolateral tubercle, like that of *E. variabilis,* large and with two (anterior and posterior) lobes, but unlike *E. variabilis* anterior lobe not bifid and pointed and posterior lobe further divided into two small pointed lobes, thus tubercle as a whole somewhat tridentate; metathoracic ventrolateral tubercle like that of *E. variabilis,* larger than abdominal ventrolateral tubercles, bifid at tip and considerably smaller than mesothoracic ventrolateral tubercle. Body with short setae, but unlike *E. variabilis,* setae present on dorsolateral aspects of segments, particularly thoracic segments; ventrolateral aspects of segments hairless as in *E. variabilis.*

Head (Figs. 21, 22) somewhat similar in shape to that of *E. variabilis* but with vertex depressed in middle and laterally not produced, width 1.05 mm. Short hairs present mostly laterally where they form irregular row. Antenna well-developed, elongate and tapering distally and broad at base, unlike *E. variabilis* with bulbous area near base. Labrum subtruncate apically, depressed in middle, with several small papillae. Maxillary and labial palpi distinct, each with three sensory papillae. Mandible (Figs. 23, 24) more or less similar in shape to that of *E. variabilis* but inner margin with seven small teeth near apex.

Spiracular atrium (Fig. 25) with ridges arranged irregularly, outer ridges touching inner ridges at two or more places.

Larva (Fig 26) of third stage or a stage next to mature stage: Similar to description of mature larva but smaller and slender. Dorsal elevations of segments more distinct. Ventrolateral tubercles small, ninth abdominal segment with one ventrolateral tubercle on each side, mesothoracic and metathoracic segments with ventrolateral tubercles forming two rows on each side; mesothoracic and metathoracic ventrolateral tubercles of equal size, the former not tridentate but simple. Body hair sparser.

Head (Figs. 27, 28) including mandibles (Figs. 29, 30) similar to that of mature larva but width 0.7 mm. Slightly less hairy. Maxillary palpus with one sensory papilla and labial palpus with two sensory papillae.

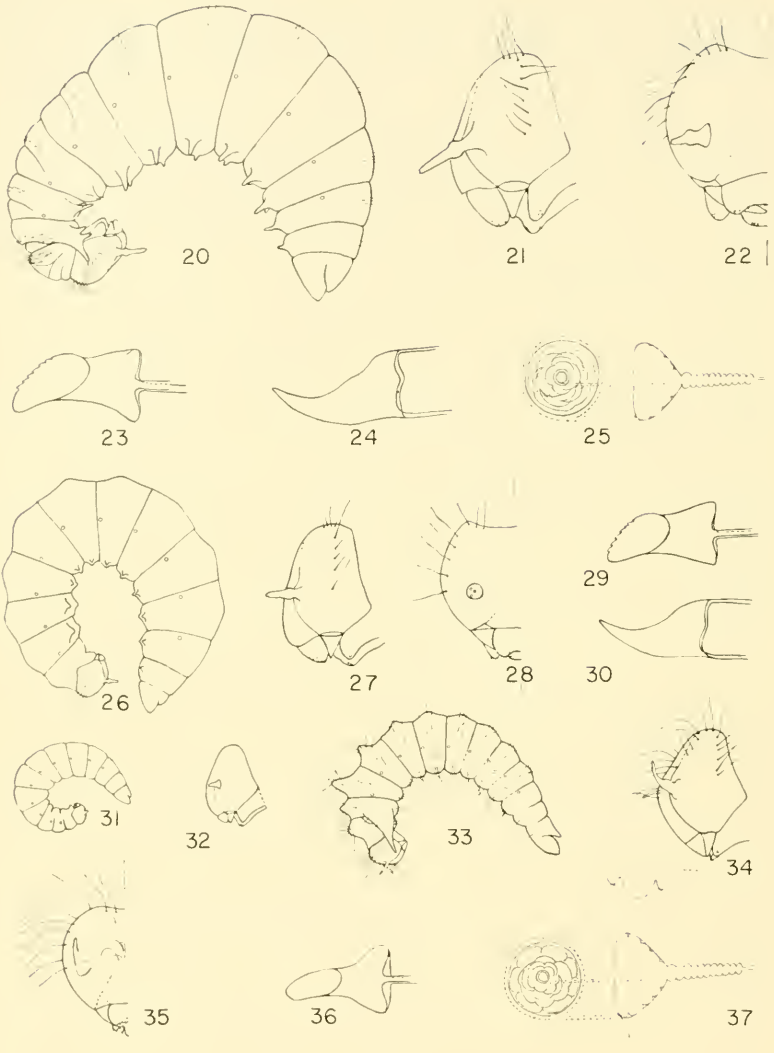
Larva (Fig. 31) probably of second stage: Similar to description of mature larva but considerably smaller, slender, intersegmental lines not complete in thoracic region. Ventrolateral tubercles absent. Body without setae.

Head (Fig. 32) similar to that of mature larva but width 0.55 mm. Antenna represented by high prominence, without bulbous area near base.

Larva of first stage not available.

Exoneura concinula Cockerell

Mature larva (Fig. 33): Slender with intersegmental lines distinct but unlike *E. variabilis* and *E. hamulata,* without additional transverse furrows. Dorsal elevations of body segments, unlike *E. variabilis* and *E. hamulata,* forming small mid-dorsal tubercles particularly on thoracic and first abdominal segments; metathorax with largest mid-dorsal tubercle; second, third and fourth abdominal seg-



FIGURES 20-37.—20. *Exoneura hamulata,* mature larva. 21, 22. Lateral and frontal views of head of same. 23, 24. Inner and ventral views of mandible of same. 25. Spiracle of same. 26. *Exoneura hamulata,* third-stage larvae. 27, 28. Lateral and frontal views of head of same. 29, 30. Inner and ventral views of mandible of same. 31. *Exoneura hamulata,* probable second-stage larva. 32. Lateral view of head of same. 33. *Exoneura concinula,* mature larva. 34, 35. Lateral and frontal views of head of same. 36. Inner view of mandible of same. 37. Spiracle of same.

ments with small mid-dorsal tubercles. Only one large ventrolateral tubercle present on each side; it is on mesothorax, and is broad basally and tapering apically, a bulbous area at base of anterior surface of ventrolateral tubercle where it joins body. Body more hairy than in other *Exoneura,* short setae present on dorsolateral and ventrolateral areas except for last three abdominal segments which lack setae dorsolaterally, and have only one or two small setae ventrally; setae on lateral aspect of body much shorter than setae of dorsal and ventral surfaces.

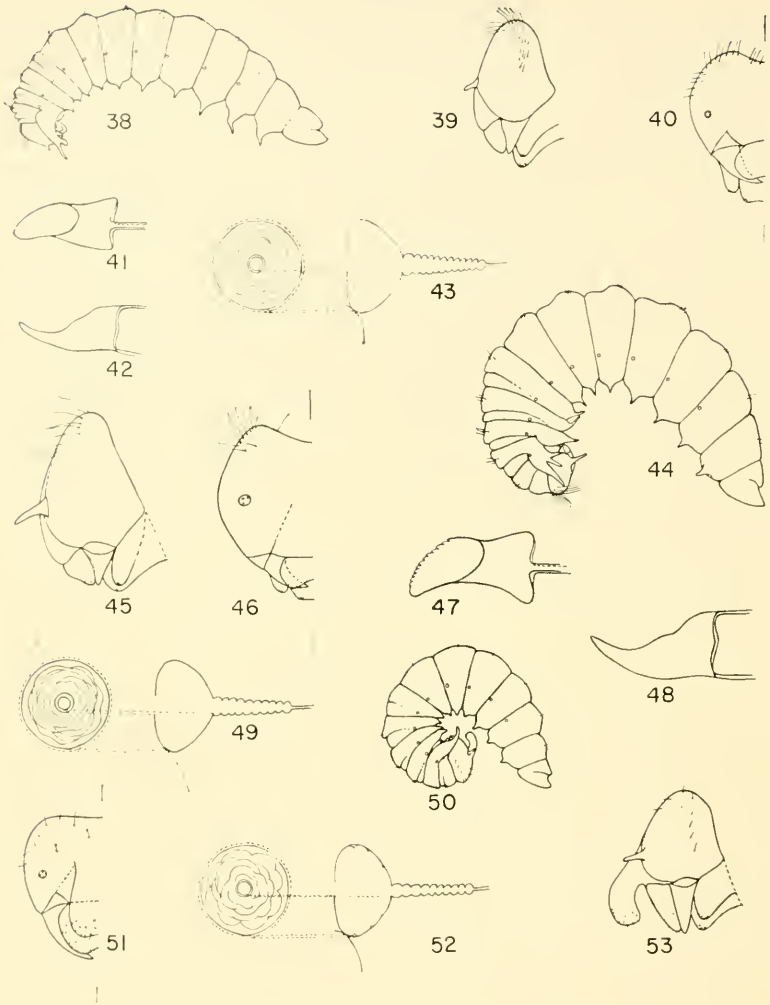
Head (Figs. 34, 35) similar in shape to that of *E. variabilis* and *E. hamulata,* without lateral projections. Hairs longer and more numerous than in *E. variabilis* and *E. hamulata* and present on frontal region as well as elsewhere. Antenna well-developed, without bulbous area near base and slightly curved upward near tip, provided with few sensory papillae. Labial palpus well-developed and distinct, provided with three sensory papillae; maxillary palpus with two sensory papillae. Mandible (Fig. 36) more or less as in *E. variabilis* in shape but more slender apically.

Spiracular atrium (Fig. 37) with ridges arranged irregularly, outer ones with spines.

Exoneura obscuripes Michener

Mature larva (Fig. 44): Slender with intersegmental lines distinct and with additional transverse furrows in thoracic region as in *E. variabilis, E. hamulata* and *I. excavata.* Dorsal elevations of abdominal segments prominent as in *E. hamulata.* Ventrolateral tubercles forming two rows on each side of body as in *E. variabilis, E. hamulata* and *I. excavata.* Prothoracic and last abdominal segments without ventrolateral tubercles, as in all other species of *Exoneura;* ventrolateral tubercle of mesothorax large and trifid, more or less like that of *E. hamulata;* ventrolateral tubercle of metathorax simple, unlike that of *E. hamulata* and *E. variabilis.* Body less hairy than *E. hamulata,* like *E. variabilis,* short setae confined to dorsal aspects of body segments; last abdominal segment hairless.

Head (Figs. 45, 46) similar to that of *E. hamulata* but with vertex slightly more depressed. Surface less hairy than in *E. variabilis, E. hamulata, I. excavata* and *E. concinula,* short hairs present dorsolaterally. Antenna well-developed, elongate, tapering distally, broad at base as in other *Exoneura* species, without bulbous area near base. Labrum subtruncate apically, with a deep notch in middle, provided with several papillae. Maxillary and labial palpi distinct, each



FIGURES 38-53.—38. *Inquilina excavata*, mature larva. 39, 40. Lateral and frontal views of head of same. 41, 42. Inner and ventral views of mandible of same. 43. Spiracle of same. 44. *Exoneura obscuripes*, mature larva. 45, 46. Lateral and frontal views of head of same. 47, 48. Inner and ventral views of mandible of same. 49. Spiracle of same. 50. *Exoneura sub-baculifera*, mature larva. 51, 53. Lateral and frontal views of head of same. 52. Spiracle of same.

with two sensory papillae. Mandible (Figs. 47, 48) similar to that of *E. hamulata* but inner margin with more teeth.

Spiracular atrium (Fig. 49) with ridges arranged irregularly, without spines.

Exoneura sub-baculifera Rayment

Mature larva (Fig. 50): Slender, with intersegmental lines distinct and with additional transverse furrows on thoracic segments and on first two abdominal segments, as in *E. variabilis* and *E. hamulata.* Dorsal elevations of segments not conspicuous except for eighth and ninth abdominal segments. Ventrolateral tubercles, unlike those of other *Exoneura* species described here, form a single row on each side of body. Prothoracic and last abdominal segment without ventrolateral tubercles; ventrolateral tubercle of mesothorax largest of all and not branched, pointed apically, broad at base as in *E. concinula;* ventrolateral tubercle of metathorax not bifid. Body almost hairless, with one inconspicuous seta present on dorsal surface of each body segment except for last two abdominal and prothoracic segments, the former completely hairless and the latter with two inconspicuous setae present ventrally.

Head (Figs. 51, 53) without lateral projections and somewhat similar in shape to other *Exoneura* but with a snout on frons. Less hairy than other *Exoneura* described here, with a few small inconspicuous setae present on dorsal and lateral aspects. Antenna as in all other *Exoneura,* well-developed, elongate, tapering distally; provided with four sensory papillae. Maxillary and labial palpi distinct, each provided with three sensory papillae. Mandible with margins toothless as in *E. variabilis.*

Spiracular atrium (Fig. 52) with ridges, and small, rather inconspicuous spines.

Inquilina excavata (Cockerell)

Mature larva (Fig. 38): Slender with intersegmental lines distinct and with additional transverse furrows in thoracic region as in *E. variabilis* and *E. hamulata.* Dorsal elevations of body segments not quite as prominent as in *E. variabilis.* Ventrolateral tubercles conspicuous and forming two distinct rows on each side of body as in *E. variabilis* and *E. hamulata.* Prothoracic and last abdominal segment without ventrolateral tubercles; ventrolateral tubercles of external row of posterior abdominal segments considerably larger than rest of ventrolateral abdominal tubercles of that row; mesothoracic ventrolateral tubercle of characteristic shape unlike other species, broad at base, somewhat bifid at tip, anterior portion tapering, posterior lobelike, an additional small protuberance near middle of postero-ventral aspect of this tubercle. Body moderately hairy as in *E. variabilis* and *E. hamulata;* thorax more hairy than abdo-

men; short setae present on dorsolateral aspects of thoracic segments; last two or three abdominal segments hairless; setae also absent on ventrolateral and ventral aspects of body.

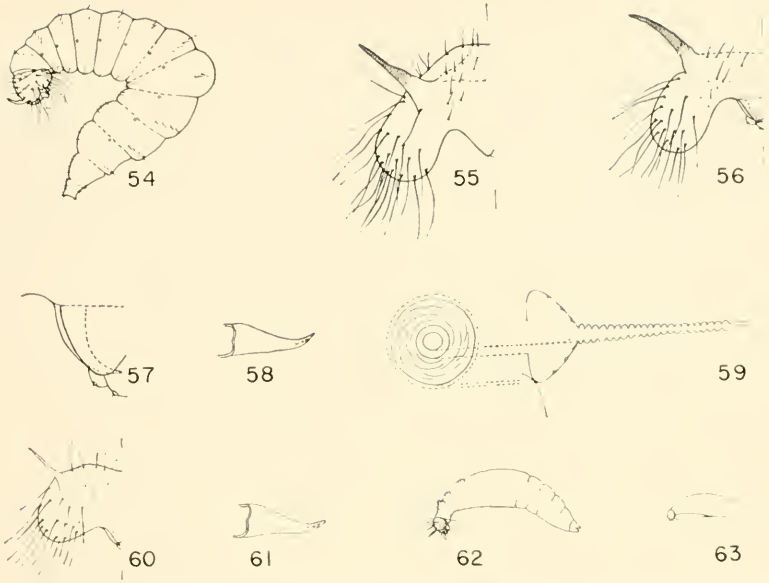
Head (Figs. 39, 40) similar in shape to that of species of *Exoneura* described here. Head less hairy than in *E. concinula*, about as in *E. variabilis* and *E. hamulata;* short setae present on lateral and dorsal aspects. Antenna as in *E. variabilis*, *E. hamulata* and *E. concinula* and provided with five sensory papillae. Labrum subtruncate apically, medially depressed, provided with several papillae, mostly apically. Labium unlike *E. variabilis*, *E. hamulata* and *E. concinula*, large, subtruncate apically, provided with two sensory papillae on each side; maxillary palpus large and distinct, provided with two sensory papillae. Mandible (Figs. 41, 42) similar in shape to that of *E. variabilis*.

Spiracular atrium (Fig. 43) with a few feeble wavy ridges and without spines.

Exoneurella lawsoni (Rayment)

Mature larva (Fig. 54): Slender, peculiarly bent at fifth abdominal segment unlike larvae of genera *Exoneura, Inquilina,* and *Allodapula.* Between many abdominal segments intersegmental lines not distinct. Dorsal elevations of body segments distinct, particularly that of fifth abdominal segment where body is characteristically bent, but eighth, ninth and tenth abdominal segments rather depressed dorsally. Ventrolateral tubercles absent, unlike *Exoneura* larvae. Body moderately hairy, short setae present on dorsum of body, ventrolateral setae present, one per segment, on thoracic and anterior abdominal segments.

Head (Figs. 55-57) of a characteristic and peculiar shape, thus very different from that of *Exoneura* larvae; laterally greatly produced and lateral projections hanging downwards in a characteristic fashion, width 0.90-1.1 mm. Surface with abundant hairs of different sizes; lateral projections with numerous long, thick hairs, dorsal and frontal regions with few and short hairs. Unlike *Exoneura, Inquilina* and *Allodapula,* labroclypeal suture inconspicuous. Antenna well-developed, elongate, tapering distally and broad at base, slightly curved upward near apex and with peculiar annulations (seen under compound microscope). Labrum strongly bilobed apically with few small papillae, mostly near apical margin of each lobe. Maxillary and labial palpi distinct, each with a conspicuous sensory papilla. Mandible (Fig. 58) very unlike that of *Exoneura,* reduced, slender and pointed apically, with small tooth-like projections laterally near apex.



FIGURES 54-63.—*Exoneurella lawsoni.* 54. Mature larva. 55, 56. Frontal and fronto-ventral views of head of same. 57. Mouth-parts of same, magnified. 58. Ventral view of mandible of same. 59. Spiracle of same. 60. Frontal view of head of third-stage larva. 61. Ventral view of mandible of same. 62. Probable second-stage larva. 63. Probable first-stage larva.

Spiracular atrium (Fig. 59) with a few feeble, incomplete, irregularly arranged ridges, inconspicuous spines. Subatrium very long, unlike *Exoneura.*

Larva of third stage or a stage next to mature larva: Similar to description of mature larva but smaller, bending at fifth abdominal segment but not as strongly as in mature larva. Dorsal elevations of body segments more conspicuous, particularly in thoracic region.

Head (Fig. 60) including mandible (Fig. 61) similar to that of mature larva but smaller, width 0.70-0.80 mm.; lateral projections bent downwards but not hanging.

Larva (Fig. 62) probably of second stage: Similar to description of mature larva but smaller, intersegmental lines not complete and even not distinct in certain body regions. Body less hairy, ventrolateral aspects of posterior abdominal segments lacking setae. Prothorax with small conical middorsal tubercle. Body not bent at fifth abdominal segment.

Head similar to that of mature larva but considerably smaller,

width 0.55-0.65 mm. Lateral projections not hanging downwards but slightly bent as in head of larva of third stage.

Larva (Fig. 63) probably of first stage: Intersegmental lines absent and body hairless.

Head similar to that of mature larva but very small in size, width 0.30-0.45 mm.; lateral projections slightly produced, not bent downwards. Hairless.

The larva and female described for *lawsoni* by Rayment (1946b) are presumed to be misidentified (see Michener, 1962).

DISCUSSION AND SUMMARY

Morphology and systematics: Brauns (1926), working in South Africa, was the first to investigate the biology of *Allodape* and its relatives. His observations revealed the extraordinary life history of these small bees. A number of eggs are laid together, not in separate cells as is the rule for almost all bees; the older larvae move nearer to the nest entrance, and pupae are found even nearer. He also recognized three types of larvae in the genus *Allodape* as understood by him, corresponding with three methods of feeding. Fundamentally, these three methods are the same, in the sense that these larvae are progressively fed by the mother bee. In Brauns' first type of larva, the thorax is provided with a pair of movable and contractile fleshy protuberances (ventrolateral tubercles), which may be called arms in accordance with their function. These arms enable the larva to retain the small morsel of food deposited between them by the mother bee, which feeds in this way a number of larvae at one visit. These armlike processes are said to hold the food until it is devoured. Brauns' example of this type of larva is *Allodape ceratinoides* Gribodo. In the second type, the larva is provided with a great number of short, fleshy and contractile appendages, disposed along the body. Friese uses the term pseudopodia for these appendages. As these larvae are placed somewhat perpendicular to the lumen of the gallery and in a cluster in the nest, it is presumed that by the aid of these fleshy protuberances the larvae are able to keep their position in the lumen of the gallery. The food is provided among the heads of the various larvae. Brauns' example of this type of larva is *A. pringlei* Cameron. The third type of larva is characterized by a still different method of feeding, in which the mother bee carries in food for only one larva at a time. The larva clings to the food mass closely and broadly with its very flat ventral surface. Only two comparatively small and inconspicuous fleshy

protuberances, the anterior larger than the posterior, are to be seen on each side of the larva. A review of the bionomics of these bees has been given by Sakagami (1960).

Australian species related to *Allodape* are currently placed in four genera, *Allodapula*, *Exoneura*, and the recently described *Inquilina* and *Exoneurella*. *Allodapula*, originally based on African species and corresponding to type II of Brauns (1926), is characterized in Africa by the habit of laying eggs in a row, attached to the wall of the burrow, as well as by larvae with a number of short fleshy protuberances as described above.

The larvae of seven Australian and Asiatic species currently included in *Allodapula* do not show the short fleshy protuberances on the bodies of the larvae as mentioned by Cockerell (1934) and Brauns (1926). Furthermore, very characteristic features of these Australian and Asiatic *Allodapula* larvae are the broadly triangular heads, and the long setae on the heads and bodies, particularly the lateral projections of the head having long curved setae. The long curved hairs on the lateral projections of the head, and also the projections themselves, facilitate the feeding, which is quite different from that of any of the three types of larvae described by Brauns (1926). In Australian species the female lays one egg at a time; when the resulting larva grows a little, another egg is laid, and the larvae are arranged in such a way that the smallest is at the bottom of the nest and the oldest near the entrance. The mid-dorsal tubercle of the first abdominal segment enables larger larvae to maintain their positions in the lumen of the gallery. Larvae of five Australian species of *Allodapula* were described by Michener and Syed (1962).

It is not now desirable to name an Australian-Asiatic genus to include these species, because there is not enough material available from Africa for comparison, and because the adults show the characters on which Cockerell (1934) erected the genus *Allodapula*.

Of the other Australian genera, *Exoneura*, *Inquilina*, and *Exoneurella*, which are related to *Allodapula*, I have been able to study larvae of seven species. The larva of *Exoneurella* fully supports the idea of separating this genus from *Exoneura* (Michener, 1962).

Most larvae of genus *Exoneura* (with *Inquilina*) possess tubercles on each side of the body on all segments except the prothoracic and last abdominal. *E. concinula*, however, lacks such structures except for a pair of large mesothoracic tubercles. By the presence of ventrolateral tubercles, most *Exoneura* larvae resemble those of

African *Allodapula* (*Allodape* larvae of type II, Brauns, 1926); *E. concinula* resembles more closely *Allodape* larvae of type I (Brauns, 1926).

The ventrolateral tubercles show differences in shape among various species of *Exoneura*. Especially the mesothoracic tubercles or "arms" provide good specific characters. Unfortunately, the fine details of structure have not been investigated by earlier authors although they show striking differences among the species of *Exoneura* and *Inquilina* described here. The mandibles of all the six species have a peculiar shape, with a spoon-like structure near the apex, but show differences in serration.

The newly-separated Australian genus *Exoneurella* has larvae which possess very characteristic features, not shown by *Exoneura* and *Inquilina* larvae, such as the absence of ventrolateral tubercles, the very characteristic hanging lateral projections of the head provided with long thick hairs, and the reduced mandibles.

The fine details of *Exoneurella* further show differences, like the annulation of the antennae, the biolobed labrum, the reduced labroclypeal suture, etc. The spiracles of the two genera also show differences; the atrium is more funnel shaped in *Exoneurella* than in *Exoneura* and the subatrium is much elongated in *Exoneurella*, unlike *Exoneura*.

Number of larval stages: To estimate the number of larval stages in *Allodapula unicolor* the emphasis was placed on presence or absence of setae, number of setae on the body, on the size of the head and also on the fine details of structures. Due to the small number of specimens of first- and second-stage larvae, measurements could not be made of many small larvae. Probably they pass through these stages rapidly so that few were found. Shape of the head in these two stages is quite different from that of the third stage and of mature larvae. There is no sign of lateral projections on the head of first-stage larvae; the head of the second-stage larva possesses slight lateral projections, and thus can be distinguished from third-stage and mature larvae. Of course the third-stage and mature larvae can be recognized by the size of the head and also by other characters. In all the various stages of larvae, the study of sensory papillae on the antennae and on the maxillary and labial palpi reveals slight differences. On the basis of the characters discussed above, I have estimated that there are four larval stages in *Allodapula unicolor* (for illustrations, see Michener and Syed, 1962). Iwata (1938) concluded, from measurements of 50 larval heads, that four larval stages exist in another species of this genus.

An attempt has been made to determine the number of larval stages in two species of the genus *Exoneura*. Unfortunately, the first larval stage is not present in the collection of *E. hamulata*. The differentiation of various larval stages has been made by the measurements of the heads and is supported by the presence, size and shape of the ventrolateral tubercles as shown in the illustrations.

The first and second stages of *Exoneura variabilis* do not show any sign of integumentary protuberances. These stages can be segregated on the basis of head width; also the second possesses intersegmental lines which are absent in the first. The third-stage larva possesses only the mesothoracic tubercle which is in the form of a small bifid protuberance. The mature larva has two rows of ventrolateral tubercles; the mesothoracic ventrolateral tubercle is very large and branched. The head widths of the larvae of these two stages show distinct differences. With all these differences, the author has been able to estimate four larval stages in *E. variabilis* and *E. hamulata*.

To gather information on the number of larval stages of *Exoneurella lawsoni*, emphasis has been placed on the same characteristics as described for *Exoneura*. Four larval stages have been recognized in this species as well.

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Behavioral Studies of Army Ants [1]

CARL W. RETTENMEYER [2]

ABSTRACT: Studies in Panama and Kansas indicate considerable diversity and variability in the behavior of army ants (Dorylinae). New observations are integrated with an extensive review of previous literature. Most species of army ants raid in narrow columns, and only two species have swarm raids with large masses of ants advancing across the forest floor. The latter "swarm raiders" capture a wider variety of arthropods for food than do "column raiders," but all army ants appear to kill more nondoryline ants than any other kind of arthropod. The army ants do not attack some species of arthropods; many species are attacked but not killed; and many species are killed but not eaten or only partially eaten. Species of army ants differ in their selectivity or specificity in capturing certain species of ants or other booty. The frequency and regularity of emigrations of entire colonies differs among species and may be partially dependent upon the degree to which the brood is synchronized in age. Some species have brood of almost all ages at one time, and these species probably emigrate less frequently than species with synchronous broods. The amount of food near a bivouac appears to affect the direction, distance, and duration of raids and emigrations but has little or no effect on whether or not a colony will emigrate. In forming their temporary nests or bivouacs the army ants often hang by their legs in clusters. The main morphological adaptations for this clustering probably are the increased length and thickness of the legs. Dead workers and the remains of booty are carried to refuse deposits a short distance away from the bivouacs. Workers of the most commonly seen Neotropical army ants are highly polymorphic. The largest workers or soldiers of *Eciton* will attack prey but never carry ants, brood, or booty. The frequency with which adult workers are carried varies inversely with their size and age and increases near the ends of emigrations. Adults, larvae, and pupae are each carried in a different manner. The worker-producing larvae of *Eciton*, *Nomamyrmex*, and *Labidus* spin cocoons, but those of *Neivamyrmex* do not. Queens always run in emigration columns and frequently workers ride on the queens. The workers are primarily attracted to and often lick the gaster of the queen. Queens and males are produced seasonally usually during the dry season or early rainy season. Mating of *E. burchelli*

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in the laboratory is described, and evidence is given which indicates *Eciton* queens mate more than once and may mate annually. An extensive section on methods for collecting and studying army ants and their guests in the field and laboratory is included.

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INTRODUCTION

This paper summarizes the literature on the behavior and biology of army ants in the Western Hemisphere and includes new observations on the behavior of these ants in Panama and Kansas. Emphasis has been placed on behavioral aspects most closely connected with the arthropods associated with the army ants in order to provide a basis for detailed studies on the biology of these arthropods.

Although other ants show varying degrees of nomadism and group-raiding, the term army ants has been used almost exclusively for members of the subfamily Dorylinae. In this paper the term army ants refers to members of the tribe Ecitonini, the main group of Neotropical army ants. In addition to having different morphological characters, army ants differ from other ants because of a combination of behavioral characters. The outstanding features of their behavior are: (1) they feed almost exclusively on animal prey which is collected by large groups of raiding workers; (2) the raiding groups are usually connected to the nest by at least one continuous column; (3) the entire colony periodically and frequently emigrates to new nest sites; (4) emigrations are largely dependent

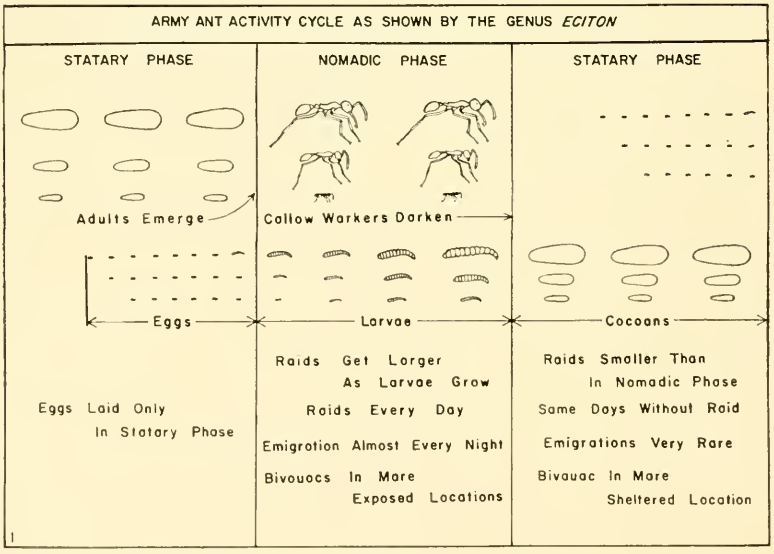

FIGURE 1.—Main features of army ant functional cycle based on behavior of *Ecitron hamatum* as determined by Schneirla.

on the size, caste, age, and range of ages of the brood (or broods)[1]; and (5) colonies are founded by division of an entire colony into two (or possibly several) daughter colonies. Although other ants may possess some of the above characteristics, apparently none possesses all of them. Moreover, a colony of army ants has a very large number of workers but usually only a single queen except at one time of the year when new queens are produced. Colonies usually have over 50,000 workers and may have over 1,000,000.

TABLE 1.—Workers of Ecitonini Examined from Barro Colorado Island.

SPECIES OF ANT	Workers other than majors	Majors	All workers	Larvae	Colonies	Samples	Samples 51+	Samples 101+
E. burchelli foreli	494,873	2,605	497,478	98,074	18	54	46	38
E. hamatum	32,517	2,207	34,724	29,939	30	52	32	28
E. dulcius crassinode	4,687	109	4,796	1,261	11	22	9	5
E. vagans mutatum	13,236	343	13,579	187	13	27	12	8
E. mexicanum panamensis	4,331	245	4,576	602	29	35	7	5
L. praedator sedulus	24,397	.....	24,397	193	22	32	22	15
L. coecus	10,727	.....	10,727	0	7	9	9	6
Noma. esenbecki crassicornis	3,481	.....	3,481	94	14	25	10	5
Neiv. gibbatus	1,736	.....	1,736	0	2	2	2	2
Neiv. humilis	622	.....	622	0	1	1	1	1
Neiv. pilosus mexicanus	3,080	.....	3,080	120	8	10	8	7
Neiv. post-carinatus	282	.....	282	0	1	1	1	1
Neiv. pseudops	231	.....	231	0	1	1	1	1
Total	594,200	5,509	599,709	130,470	157	271	160	127

1. The term "brood" follows the usage of Schneirla (1949b: 7, etc.) which is different from the common use of the term when referring to other social insects. The eggs of most species of army ants are laid in large numbers in a relatively short period of about ten days, separated by periods of about two or three weeks in which no eggs are laid. As a result, the immature stages from each batch of eggs are approximately the same age within a colony and are referred to as a brood (or synchronous brood). Colonies can have two distinct broods at one time if the development of one brood lasts long enough to overlap partially a second. Where large numbers of most developmental stages are found simultaneously within the same colony, the brood will be referred to here as a nonsynchronous brood.

Based on his research, Schneirla (1938, 1957a) has proposed a theory of cyclical functions which he maintains is applicable to an appreciable extent throughout the Dorylinae. In his publications, Schneirla has concentrated on the species *Eciton hamatum* and *burchelli* which have a distinct cycle of alternating nomadic and statary phases. This cycle is diagrammed in figure 1 which indicates how these phases and other behavior of the ants are correlated with the ages of broods. The behavior of *Eciton hamatum* will be discussed first in some detail, since this species has been most extensively studied, and its behavior comes closest to a diagrammatic "textbook example" of the army ant activity cycle. Following this, the behavior of other species of army ants, primarily from Panama and Kansas, will be discussed in less detail with emphasis on

TABLE 2.—Workers of Ecitonini Examined from Other Localities.

SPECIES OF ANT	Workers other than majors	Majors	All workers	Larvae	Colonies	Samples	Samples 51+	Samples 101+
E. burchelli parvispinum	21	0	21	0	1	1	0	0
E. burchelli foreli	6,020	122	6,142	0	3	3	1	1
E. burchelli urichi	7,338	25	7,363	341	15	15	4	2
E. burchelli cupiens	6,501	101	6,602	0	2	2	1	1
E. hamatum	10,072	213	10,285	10,000	4	4	1	1
E. lucanoides conquistador	120	0	120	0	3	3	0	0
E. vagans angustatum	2,000	1	2,001	0	2	2	1	1
L. praedator	559	.....	559	50	4	4	1	1
L. coecus	617	.....	617	500	5	5	3	2
Noma. esenbecki	50	.....	50	0	4	4	0	0
Noma. hartigi	642	.....	642	0	2	2	2	1
Neiv. legionis	250	.....	250	0	1	1	1	1
Neiv. nigrescens	14,232	.....	14,232	74	5	14	10	8
Neiv. opacithorax	1,137	.....	1,137	0	6	6	4	3
Neiv. pilosus	208	.....	208	0	4	4	1	0
Neiv. sumichrasti	86	.....	86	0	2	2	0	0
Total	49,853	462	50,315	10,965	63	72	30	22

differences from and similarities to the behavior of *E. hamatum*.

Working with army ants is rather different from studying most other ants, and experience has shown that these methods, though simple, are not obvious. Consequently, this paper includes a section on methods for collecting and studying the army ants and the arthropods associated with them.

Preserved samples of approximately 800,000 workers and larvae were examined for myrmecophiles, and samples of at least 200,000 living workers were examined in the laboratory in Panama. These samples came from about 200 colonies including those from 63 colonies sampled by other collectors at various localities. A summary of the numbers of workers, larvae and colonies is given in tables 1 and 2. All samples listed in these tables were counted completely except for ones with eggs and young larvae. The number of samples including more than 50 and 100 adult workers are also given.

DISTINGUISHING ARMY ANTS FROM OTHER ANTS IN THE FIELD

Since many other species of ants can be found in columns or clusters, it is important to be able to distinguish the army ants, or tribe Ecitonini, in the field. For this purpose, a combination of morphological and behavioral characters is most useful.

Most army ant workers are under eight millimeters in length; and therefore, many species of ants, including species commonly killed by army ants, are larger than the dorylines. Sometimes people hesitate to collect army ants, because the ants have a reputation for having severe stings and bites. The fierce reputation of army ants is based almost exclusively on the behavior of only three of about 140 species. Even though workers of all species have stings, these are too weak to puncture human skin in most cases. The largest species of army ants, those of the genus *Eciton*, with workers up to 14 mm. long, have fairly weak stings. The majors or largest workers of all species of *Eciton* (except *rapax*) have disproportionately large, hooked mandibles, which inflict painful bites. However, it is possible to collect and study these ants readily without receiving any stings or bites, and they are not nearly as hazardous to work with as the honeybee. Many nondoryline ants of comparable size have bites or stings which are more severe than those of the Ecitonini.

The workers of both *Eciton* and *Labidus* exhibit a great amount of polymorphism. *Eciton* workers range in length from four to 14

mm. *Labidus* workers range from two to 13 mm., and the largest workers have disproportionately large heads as in figure 2, but the mandibles are not long and hooked as in *Eciton*. *Neivamyrmex* workers range from two to six millimeters in length, and *Nomamyrmex* workers, from three to 12 millimeters. However, in the latter two genera, the size range within any one species is more limited, and there is little allometry with respect to head size.

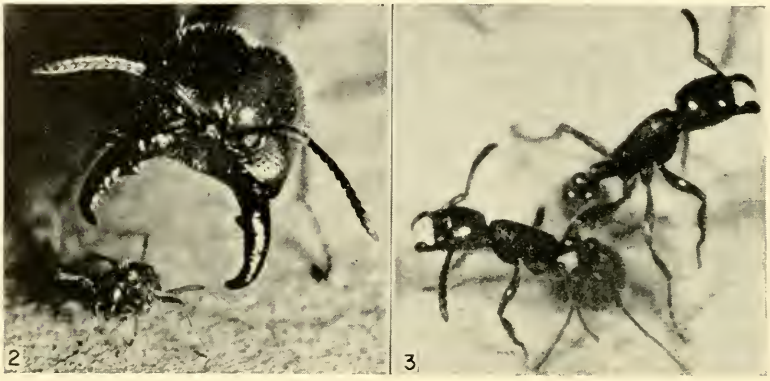

FIGURE 2.—Large and small workers of *Labidus coecus* showing almost greatest size range and head enlargement within Ecitonini.

FIGURE 3.—Excited "guard workers" of *Neivamyrmex opacithorax*. Note open mandibles, antennae extended laterally and above head, and front legs off floor of laboratory nest. Maximally stimulated workers hold their bodies even more nearly vertical than worker on right.

The compound eyes of all the workers of Ecitonini are reduced to a single pair of external facets which look like ocelli except for their lower and more lateral position. The eyes of the smallest workers are further reduced to a spot in the integument without a distinct convex cornea, or the eyes may be completely absent. None of the workers has ocelli. If facets can be seen on the surface of an eye of a worker ant, the ant is not an army ant. In addition, the petiole of the worker consists of two segments approximately equal in size and shape; the frontal carinae do not extend over the bases of the antennae; the legs are relatively long, and on the under surface of the hind tibia there is a lighter-colored stripe or elongate spot.

Army ant colonies are frequently found by hunting for columns of ants running along the ground. With practice, one can distinguish these ants from other ants in most cases by the manner in which they run. Their legs are long, and the ants run quickly and steadily in distinct columns without many workers deviating from

the trail. There are few or no workers standing still, unless the column is a strong emigration column and guard workers are present. As the ants run, the antennae are held in front of the head and curved close to the ground as in figures 8, 9, and 22. The abdomen is also kept close to the ground and never is turned up at the tip or turned over the thorax. Sometimes "guard" workers may stand at the edges of the column with their front legs off the ground as in figure 3. In this position, they normally have their mandibles open and their antennae extended above their heads. These workers can be found anywhere in a column, but usually are where the workers are especially disturbed or excited, such as at the edges of emigration columns. They may indicate the position of the queen or a nest.

All objects which the Ecitonini carry are held *under* their bodies. This behavior will distinguish these ants from many others, especially the leaf cutters. (See figures 8 to 12 of *Eciton burchelli* carrying worker larvae and booty.) A few species will occasionally eat nutmeats, vegetable oils, or fruit. However, if large numbers of ants are seen carrying leaves or other plant parts, the ants are not Ecitonini. If army ants are carrying anything, it almost invariably is part of an arthropod and most commonly is the brood of ants or wasps. The Ecitonini do little digging as a rule and if they transport dirt, it is only for a few centimeters.

The ability to distinguish whether the brood is that of army ants is of major importance for distinguishing emigration from raid columns and thus for finding bivouacs. Fortunately, no species of army ant is known to carry off the brood of any other species of army ant. Therefore, if the brood is all the same approximate age and there is a considerable amount of brood, it is almost certain to be that of the army ant species carrying it. The army ants usually carry their own larvae by grasping the thoracic segments, whereas ant larvae which are booty are frequently carried by the posterior ends. The army ant brood seen is usually all larvae, but there may be cocoons with mature pupae in them along with young larvae and eggs. There may be large larvae and some cocoons with larvae or prepupae in them. It would be extremely unusual to see pupae being carried at the middle stage of their development, since at that time the colony is normally statary. Only in colonies of the genus *Labidus* can one find brood of all ages at the same time.

In addition, the larvae of Ecitonini have a characteristic appear-

ance. Detailed descriptions of several species have been published by G. C. Wheeler (1943). The larvae are relatively long and slender with a curved, more narrow anterior end. They have heads which are larger or about the same size as the segments to which they are attached, unlike many ant larvae which have relatively much smaller heads. The larvae are white and covered with inconspicuous setae, and there are no tufts or much longer setae among the pile-like covering. Although the larvae are usually approximately the same age, there may be a fairly large range in size among the more polymorphic species. The genus *Neivamyrmex* has pupae which are not enclosed in cocoons, but the genera *Eciton, Labidus,* and *Nomamyrmex* have cocoons. If a column of army ants is transporting brood of another species of ant, this brood most frequently varies more in size and age; and parts of adult ants or entire dead ants which are carried often appear to be the same species as the carried pupae. Rarely a raid column of army ants can be found in which several hundred larvae of one species of ant prey are being carried. However, these will appear in a group preceded and followed by army ants without booty or with different booty. If the larvae are those of the army ants, there will be thousands of them, and they will be carried along an emigration route for a period of several hours.

Among the dorylines only the males have wings, but these wings normally drop off after the males have flown from their parent colony. Most males are collected at lights where one may wish to distinguish them from other male ants. Since some males lose their wings at lights, one should look around on the ground below a light for dealate males. The males of different species range from about seven to 23 mm. in length. As a rule, they are about twice the length of the largest workers of their species. All Neotropical doryline males have a similar appearance and are quite easy to distinguish from other male and queen ants. Their color varies from yellow-brown or orange, to dark brown, red-browns or black. They have large mandibles, large compound eyes and three large ocelli. The large eyes and ocelli will readily distinguish dealate males found in columns from queens, since the queens have eyes similar to those of the workers. The head is attached low on the thorax and is often hidden under it in dorsal view. The thorax is elongate or rectangular in dorsal view, not spherical. The strongly curved dorsum of the thorax and the low position of the head give the males a humpbacked appearance. There is a distinct

constriction between the propodeum and the petiole. The petiole consists of a single large segment which frequently lacks the distinct dorsal node found in most ants, but may have a pair of large lateral nodes. Moreover, the petiolar segment is often so large and closely appressed to the gaster that it appears to be part of the gaster itself. The abdomen is an elongate cylinder, usually about three times as long as it is thick or wide. The genitalia may become more extruded several days after emergence or following flight. Thus, within the same species, the external genitalia may or may not be conspicuous.

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LOCATIONS OF FIELD WORK

Canal Zone Biological Area

The arthropods associated with army ants were studied at the Canal Zone Biological Area primarily from 11 February to 19 August 1956 by the author and his wife, Marian E. Rettenmeyer. Less detailed observations were made from 31 January to 7 June 1952 while I was assisting Dr. T. C. Schneirla in studies of army ant behavior.

Similar work from 25 January to 31 March 1955 allowed more time to collect and study myrmecophiles, and extensive sampling of the refuse deposits was done during this period.

The Canal Zone Biological Area was selected as the site for this study for several reasons. This location can be easily reached from any part of the United States within two days. The area is ideally suited for work with army ants because of the combination of excellent permanent field laboratories adjacent to a tropical forest with an extensive system of trails. Army ant colonies are abundant, and a colony of some species can usually be found within several hours at any time of year or day. In addition, Dr. T. C. Schneirla or his associates have investigated the behavior of army ants there intermittently since 1932.

The Canal Zone Biological Area is a biological preserve comprising all of Barro Colorado Island. This island is approximately in the center of the Canal Zone between 9° 8′ and 9° 11′ north latitude and between 79° 49′ and 79° 53′ west longitude. The region became an island in 1914 when the Chagres River was dammed to form Gatun Lake as part of the Panama Canal. It has been a biological preserve since 1923 and at the present time is administered by the Smithsonian Institution. The island has an area of about six and one-half square miles or almost 4,000 acres. It is about three miles in diameter with a shore line at least 25 miles long. There are a few small clearings, but about half the area is covered by primeval forest, and the other half is second growth 40 to 100 years old. Enders (1935: 387-388, plate 1) has discussed the ages of the different areas of the forest and published a map based on the height of the trees about 1930. The forest is frequently called jungle or rain forest, but it is more accurately described as "evergreen seasonal forest," which is an intermediate formation between the true tropical rain forest and the semi-evergreen and deciduous seasonal forests as classified by Beard (1944, 1955). An excellent system of permanent trails extending throughout the island greatly facilitates the finding of ant columns and the subsequent tracking of the routes the ants follow. In addition, numerous streams radiate from the center of the island to the coast, and these can be used, especially in the dry season, to supplement the trails.

There is a well-defined, but not too severe dry season from about January to April when the mean rainfall is less than three inches per month. Often there is less than one-half inch of rain during each of the driest months of February and March. During this

period some of the trees lose their leaves, the leaf litter becomes dry, and the clayey soil cracks. The rainfall of the rainy season months from May through December is usually ten to 20 inches per month. A graph of mean monthly rainfall for 1925 to 1939 is given by Schneirla (1949b: 12). The months of January and April are quite variable and can be considered either dry or rainy season depending upon the rainfall of the specific year. Since there were 5.57 inches of rain in January 1956, including over two inches in the last week of the month, this month should not be considered typical of the dry season. However, it was considerably drier than the previous months. During February, March, and April between 2.1 and 2.6 inches of rain fell each month, which is slightly above the average precipitation, and the relatively even distribution of the rain made the dry season of 1956 a moderate one. The dry season of 1952 was more pronounced with rainfall totals for January through April of 2.40, 0.39, 0.11, and 5.46 inches, respectively. In 1955 the dry season had a more gradual beginning and lasted longer. In December 1954 only 7.25 inches of rain fell, which is rather low for that month. The months of January through April had respectively 9.05, 0.46, 0.90, and 0.37 inches.

Observations were thus made during most of the dry seasons of three years, during the transition period from dry to rainy season in two years, and during early rainy season in one year. No observations have been made during the rainy season after 19 August. (Dr. Schneirla and Dr. and Mrs. R. Z. Brown have observed the army ants during this period on Barro Colorado Island.)

Additional information on Barro Colorado Island and its ecology has been presented by Allee (1926a, 1926b), Chapman (1929, 1938), Enders (1935), Kenoyer (1929), Moynihan (1959), Standley (1933), Williams (1941), and Woodring (1958).

Vicinity of Lawrence, Kansas

In Kansas, army ants were observed without my making any attempt to follow individual colonies. Several colonies were found within the city limits of Lawrence, Kansas, or on the campus of The University of Kansas. These are residential areas having houses alternating with large lawns with scattered trees. No extensive cover by trees or shrubs exists near the sites where the ants were seen. Several other colonies were found in or near open fields, part of which were cultivated at the time. In these areas there also was little tree cover, but fewer buildings, roads, etc., that might hinder

the ants' emigrations or raids for food. A few colonies were found at The University of Kansas Natural History Reservation. This is an area primarily of eastern hardwood forest with some areas of grassland. Colonies were found in both the woodland and in the open fields. General information about this reservation and the areas where the colonies were found has been published by Fitch (1952). These parts of Kansas receive a mean annual precipitation of about 35 inches. The only genus of army ants found in Kansas is *Neivamyrmex*; its range extends only about 200 miles north of Lawrence.

METHODS FOR STUDYING ARMY ANTS AND MYRMECOPHILES

Identification of Species of Army Ants

Since the behavior of the army ants varies according to the species, it is useful to be able to recognize the species of ant in the field. Often several colonies of different species may be located in one day, and one may wish to study the rarest species first or to study the species most likely to have certain myrmecophiles living with it.

The odors of the various species are different but impossible to describe adequately. The more distinctive odors, such as that of *E. mexicanum*, can be useful aids in identification, especially at night in the field or when columns are so weak that only a few intermediates can be found. If one rolls a worker between one's fingers, the ant can neither bite nor sting, and the odor is more readily apparent.

Keys and descriptions for all species and known castes of army ants have been published by Borgmeier (1955). The following key was modified from those of Borgmeier with the addition of some characters to make it more useful for field identification so that with a hand lens one can identify the species of the more common army ant workers in Panama. The key is easiest to use if both majors and small workers can be examined in the dry state rather than in alcohol.

Key to Workers of Common Army Ants in Panama

1. Ants found in a column or nest or location unknown . . . 2.
   Ants found in a swarm raid (advancing mass of ants one meter to ten meters wide) . . . 10.
2(1). Antennae thick, scape about one third as wide as long . . . 3.
   Antennae slender, scape less than one fourth as wide as long . . . 4.

3(2). Propodeum with two broad, flat, transverse dorsal carinae.
Nomamyrmex esenbecki (Westwood).
Propodeum rounded posteriorly, without carinae.
Nomamyrmex hartigi (Westwood).

4(2). Tarsal claws without tooth; largest workers 5 to 7 mm. long; relative size of head (compared with body) same for largest and smallest workers.
Neivamyrmex sp. (*pilosus* is most common species).
Tarsal claws with tooth; largest workers 8 to 12 mm. long; heads of largest workers disproportionately larger than bodies, in comparison with smallest workers ..... 5.

5(4). Majors with elongate, hook-like mandibles (ice-tong-shaped) usually without teeth; heads of all workers dull (except majors of *E. hamatum*) (specimens should be dry to determine if heads are dull or shiny) ..... *Eciton* 6.
Majors with triangular, toothed mandible; heads shiny . *Labidus* 12.

6(5). Small workers with thorax brown to reddish-black, gaster orange or much lighter ..... *Eciton burchelli* (Westwood).
Small workers with thorax yellow to brown, gaster same color as thorax or only slightly lighter ..... 7.

7(6). Light brown to yellow 8
Brown to reddish brown ..... 9.

8(7). Hind tibial spur about four times as long as wide and about as long as width of distal end of tibia; petiole with blunt anteroventral spine or without spine; majors with shiny heads.
E. hamatum (Fabricius).
Hind tibial spur about as long as wide, much shorter than distal width of tibia; petiole with long sharp, anteroventral spine; majors with dull heads ..... *E. lucanoides* Emery.

9(7). Propodeal spines blunt, notch between spines shallow (more like a carina with a median indentation than pair of spines); majors 9 to 10 mm. long. ..... *E. mexicanum* Roger.
Two sharp propodeal spines distinctly separated by narrow, deep, V-shaped notch; majors 11 to 13 mm. long. ..... 10.

10(9). Majors and larger intermediates with spine on occipital angle of head (can be felt by rubbing finger over occipital area of head) ..... *E. vagans* (Olivier).
Majors and larger intermediates without spine on occipital angle of head ..... *E. dulcius crassinode* Borgmeier.

11(1). Heads not shiny; majors 10 to 12 mm. long; mandibles longer than width of head and hooked (ice-tong-shaped); small workers with thorax reddish-black, gaster orange or much lighter.
Eciton burchelli (Westwood).
Heads shiny; majors 8 to 10 mm. (rarely 12 mm.) long; mandibles shorter than width of head; mandibles triangular and toothed; thorax same color as gaster ..... 12.

12(5, 11). Color dark brown to black or reddish-black; petiole without anteroventral spine ..... *Labidus praedator* (F. Smith).
Color reddish-yellow to reddish-brown; petiole with anteroventral spine ..... *L. coecus* (Latreille).

Methods for Finding Nests or Bivouacs

Since army ant columns are normally continuous, it is theoretically possible to follow any column to the nest. If it is a raid column, one can follow it in one direction to find the advancing front, or in the opposite direction to find the nest. If the ants are emigrating, the column will lead from the old to the new bivouac. Therefore, it is useful to know first whether a column is a raid or emigration column.

Raid and emigration columns can often be distinguished on the basis of the amount and consistency of the traffic. Raid columns usually show frequent waves or spurts of traffic and at times there may be gaps of one or two meters along the route where there are no ants. The rare gaps in emigration columns seem to be caused by some direct disturbance of the column. The emigrating ants run with a more even pace, showing no hesitation, and about 90% generally are going in one direction. In addition, raid columns of the more epigaeic species, *E. burchelli*, *E. hamatum*, and *L. praedator*, are one to five ants wide as a rule, whereas the emigration columns are five to ten ants wide. The more subterranean species commonly have raid columns one to three ants wide and emigration columns two to five ants wide. If ants are running in both directions along a column, in more or less equal numbers, it is almost certain to be a raid column. However, if they are mostly going in one direction it could be either a raid or emigration route. Raid columns are not apt to have guard workers or ant roadways.

Different species of army ants start raids, and the emigrations which may follow raids, at different times of day. Since raids of nomadic colonies of *Eciton hamatum* and *burchelli* typically start about dawn (Schneirla, 1938, 1940), most columns of these two species until about 8:00 a. m. have ants moving primarily away from the bivouac without carrying any booty or brood. Any objects being carried by the workers at this time of the morning can be expected to be booty being carried toward the nest. The best time to find columns and nests of these two species is between 9:00 and 11:00 a. m. Then the raid columns are longer than earlier in the day, increasing their chance of being found. They also are wider with more ant traffic, including more booty carriers which are virtually all returning to the nest, making the columns easier to trace. Where ant columns fork, these booty carriers are of considerable importance in indicating the direction to the bivouac. If no booty carriers are present, one can deduce the direction of

the nest with less certainty by the direction of most ant traffic and the angles of the fork. In most cases the angle between the two outward branches is more acute than the angles between either of these and the basal column leading to the nest. If several columns can be seen close together, the predominant traffic on all of them is most apt to be moving in a consistent direction (either all away or all toward the nest).

About 11:00 a. m. there is a decrease in traffic away from the bivouac on columns of *hamatum* and *burchelli,* and more workers both laden and unladen return to the bivouac. During the siesta period between about 11:00 a. m. and 2:00 p. m., columns of all the species of army ants, even the most epigaeic species, *E. burchelli* and *hamatum,* are difficult to follow to the bivouac. Columns are thinner or absent, and booty may be deposited in caches rather than carried back to the bivouac. Thus, booty may be seen being carried both toward and away from the bivouac.

In late afternoon and early evening there is frequently an increase in raiding activity. If most ants are carrying booty, and they are running in a consistent direction in thin columns of about three ants wide, these ants most probably are returning to the bivouac. If the column is wider with booty being carried in both directions, it probably is the start of an emigration route. Later booty will be carried away from the old bivouac in increasing amounts and more unladen workers will be running in even wider columns away from the old bivouac. By the time brood is seen in the column, the new bivouac is usually being formed. Although workers carrying booty may be scattered throughout an entire emigration, they are more concentrated at the beginning.

If an emigration is going to occur, there will be an increasing exodus of ants from the old bivouac, and a large number of these will be carrying larvae (or occasionally eggs or cocoons). Emigrations of *hamatum* usually begin between 3:00 and 6:00 p. m. and end between 6:00 and 9:00 p. m. Emigrations of *burchelli* may begin between 3:00 and 9:00 p. m. and end between 10:00 p. m. and 4:00 a. m. Rarely, they start and end later. Therefore, between 6:00 and 8:00 p. m. is an excellent time to hunt for these two epigaeic species.

Colonies of the two swarm raiders, *E. burchelli* and *L. praedator,* can sometimes be located by the noise of the flies and ant birds which accompany swarm raids (see section Raids of *Eciton burchelli*). On two occasions I have found bivouacs of *burchelli* by

tracing the odor coming primarily from the refuse deposits next to the bivouacs.

Since the activity of the more subterranean species of army ants cannot be as consistently predicted by the time of day, it is more difficult to determine whether their columns are raid or emigration columns. However, the time of day is of some help in addition to the differences (given above) in the appearance of the two types of columns. The subterranean species raid primarily in the evening, at night, or in the morning before 10:00 a. m., and emigrations may follow these raids. Booty being carried in both directions along a column may indicate an emigration is beginning. Emigrations were never seen during the warmest parts of the day, and rarely in the morning. If an emigration column is seen in the morning, it probably will become weak and stop before about 10:00 a. m. unless the day is cloudy or rainy. Columns of the hypogaeic species are more often found during rainy days or in the rainy season. However, both raid and emigration columns may go underground a few to many meters from the actual bivouacs which are subterranean or in sheltered places, such as rotten logs. One can often determine whether the bivouac is near the hole into which the ants disappear by pounding or jumping on the surrounding ground. If ants pour out of the hole, the bivouac or a large cluster of ants is almost certain to be only a few centimeters below the surface. If no ants appear by this technique, it is usually futile to dig where the column disappears into the ground. One may be able to find the bivouac by investigating appropriate sites in the vicinity. These may be logs (under or inside), hollow trees, cavities under stones or large roots, spaces between buttresses of trees, brush heaps, and areas of dense vegetation such as the bases of clumps of bamboo, palms, or terrestrial bromeliads (wild pineapple).

Mounds of dirt at the edges of logs or rocks can be useful indicators of ant activity which might be due to Ecitonini. All species of army ants are capable of digging, but normally the epigaeic species do not do so. The subterranean species apparently never dig complete nests but probably always do a little digging at their bivouac sites. Species of *Eciton, Labidus, Nomamyrmex,* and *Neivamyrmex* have all been observed to enlarge either their bivouac sites or the holes through which their columns enter the ground. If these ants remove a large quantity of dirt, they pile it in loose

mounds which do not extend more than a few centimeters from the entrance to the bivouac.

In addition, *Labidus* and *Nomamyrmex* may make dirt passageways for raid or emigration columns. These passageways differ from those of termites in that the earth is not cemented together in any way but is simply piled up. The passageways may be open at the top or some parts of them may be completely closed to form tunnels as in figure 21. Such tunnels without ants in them during the daytime may contain ants at night. One species of army ant, *Nomamyrmex hartigi*, has been reported raiding termites inside the tunnels made by the termites on the sides of trees and on other surfaces.

Searching for columns is the easiest way to find the maximum number of colonies of army ants in a tropical forest like that on Barro Colorado Island. However, the rarest species are subterranean and are more apt to be found by cutting open rotten wood, turning over rocks, logs, etc., than by finding columns. On one occasion the cutting open of a log containing a bivouac of *E. hamatum* revealed a bivouac of *L. praedator* within the same log. No column nor swarm of the *praedator* colony was seen around the log before the bivouac site was cut apart. On another occasion a sample of army ants was unknowingly included in a sample of leaf litter put into a Berlese funnel. This small species of *Neivamyrmex* was apparently raiding on or near the surface of the soil under leaves.

Turning over stones, especially if there are piles of loose dirt around them, is the most successful way in my experience for finding colonies of army ants in temperate regions. Ecitonini in temperate regions place their larvae under stones like many nondoryline ants presumably because of the warmth retained by the stones. If these ants disappear from under a stone in the evening, the next day they may return to the same spot.

Schneirla has used string to mark the positions of bivouacs and to indicate the emigration routes. One can avoid losing an ant colony or becoming lost oneself in the tropical forest by using such trails of string. Trails of vegetation, such as palm fronds, take much more time to make and are more disturbing to the ants. Some kind of trail is necessary for one to be able to relocate the bivouacs especially at night. If one wishes to indicate the route more precisely, the string can be put only a few centimeters away from the ant trail and always to the same side of the trail when

moving away from a bivouac. For more accurate indications of the route, toothpicks have been used most successfully. I have also used spots of colored paint next to the trail, but the ants were disturbed by the odor of aromatic paint solvents. Toothpicks were used to mark trails to refuse deposits by placing the toothpicks two centimeters to the right of the center of the column. Colored or marked toothpicks were used to indicate particular places along these columns.

Measurements of Distances

The distances between bivouacs reported in this paper were estimated by using the trail markers on Barro Colorado Island as guides and by pacing off the route taken in following the colony to its new bivouac. This method apparently has been used in most cases by Schneirla. Therefore, the distances are neither the shortest distances between any two bivouacs nor the distances that the ants actually traveled. No accurate measurement has apparently been made of the distance an ant travels on an emigration. Without including possible backtracking toward the old bivouac, the more zigzag path of an individual ant could easily be two or more times the distances reported in this paper.

Dimensions of bivouacs and lengths of refuse columns are based on actual measurements.

Methods for Sampling Ant Colonies

When a colony is found for the first time, one usually wishes to know the age and sex of the brood in order to predict the emigrations and other activity of the colony. The methods used for these predictions are given below in the section entitled, Determining Ages of Broods and Position of Colony in Activity Cycle. However, the way in which a sample is taken affects not only the estimate of the brood's age but also the number of myrmecophiles in the sample.

When a colony was first found, its bivouac was usually partially knocked down with a machete, and the brood and workers sampled. Samples were usually taken by picking up clusters of ants with forceps 25 to 30 cm. long and putting these clusters directly into 70 percent alcohol. On a few occasions attempts were made to etherize bivouacs, but the ether immediately excited the ants. The bivouacs fell from their supports, and the ants dispersed through any slight openings that were not plugged tightly before the ether was applied. A much more successful method was to collect the ants as quickly as possible using a large polyethylene plastic bucket

into which they could be knocked or scraped. Where it was necessary or most efficient to use one's hands for scraping up the ants, leather gloves were useful equipment. The majors can bite through them but not deeply, and the stings cannot penetrate the leather. Cloth wrapped around the wrists prevented the ants from running up open sleeves. These latter methods were used only when I attempted to collect entire colonies or when a bivouac in a difficult location had to be thoroughly torn apart. Normally samples of any size can be taken if one grasps the ants with forceps using no protection against stings. Since the brood is primarily lying on top of the workers, a large bolus of workers from the center of a bivouac will usually include much brood. A mixed cluster of workers and brood can be picked up with forceps with no noticeable injury to the larvae.

Schneirla has reported that the brood in colonies of *burchelli* and *hamatum* is placed in the bivouac in approximate order of size: the eggs or smallest larvae being in the center, the largest larvae at the periphery. This appears to be true in compact bivouacs. However, if the bivouac contains much vegetation or is of the "compound" type (Schneirla, Brown and Brown, 1954: 273, 277), the brood may show little arrangement and be widely scattered throughout the bivouac. For these reasons, it is advisable to sample the brood from several areas of each nest rather than from a single spot if one wishes to get the most accurate picture of the size range.

Colonies of *Labidus* should be more thoroughly sampled from many parts of the bivouac, because this genus is most likely to have brood of all ages within a single nest. Since there are some indications that some myrmecophiles are found most frequently with brood of a certain age, this sampling technique may yield a greater variety of myrmecophiles. Myrmecophilous insects in general are decidedly more abundant with eggs and larvae than with cocoons and adults of the ants.

The brood of subterranean army ants may be scattered throughout much dirt or wood, or it may be partially sorted by size or age. Some sorting by size was noted in a colony in a rotten log, probably because the ants could enter the smallest passageways with only the smallest brood. Thus, one should examine all size passages for some may contain only eggs or young larvae belonging to the same brood or an additional brood of the colony. Similarly the ants which may place their young under stones may have additional

brood or brood of a different age deeper in the soil. Except for the more peripheral position of the larger (but not necessarily older) larvae in bivouacs of *hamatum* and *burchelli*, there does not seem to be any distinct arrangement of army ant brood according to size. However, so few subterranean bivouacs have been examined that it is impossible to state if the brood is placed in a regular position or arrangement within the bivouac. When two broods of distinctly different ages are present, such as the pupal and egg broods in a late statary colony of *E. burchelli*, the broods are usually completely separate. Thus, in statary colonies or colonies with a cocoon brood, one should always look for a brood of eggs.

Different ages or sizes of adult workers can be collected by several sampling techniques. The smallest workers do not seem to be common in raid columns or refuse columns. However, in the bivouac these workers are usually concentrated around the eggs, and the queen often is completely surrounded by a tight mass of over 1,000 small workers. If one tears a bivouac apart in searching for the queen, she is apt to move away from her original location in the bivouac. Most of the numerous small workers then do not stay with her, and there is a larger number of excited major workers around the queen. These dense masses of either small workers or majors are the best indicators of the location of the queen within masses of ants. Although the workers are greatly excited by their queen and attracted to her, I know of no successful method for attracting and capturing large numbers of workers by using a queen as bait.

Each colony usually has a single queen except at the time when broods of males and queens are produced. It is possible that some species, especially the more rarely found subterranean army ants, normally have more than one functional queen. Six to 12 queens but no males have been found in colonies of *Neivamyrmex carolinensis* (Schneirla, 1961: 5, Rettenmeyer and Watkins 196—).

It is sometimes desirable to collect numerous major workers since these have more myrmecophiles on them than small workers. A sample of over 90% majors can be collected easily from a bivouac of *E. hamatum* by brushing a pair of long (25 to 30 cm.) forceps lightly over the ants. Holding a major by the tips of the forceps also seems to help arouse the other majors which run up the forceps and bite them or cling to the other majors. A small cluster of five to ten majors is then transferred to a bottle before they have time to run to the top of the forceps. This technique does not work as

well with *burchelli*, possibly because the proportion of majors is lower, and the smaller workers are more aggressive than those of *hamatum*. With other species of *Eciton*, this technique has not been adequately tried. A similar technique of lightly brushing a major worker held in forceps along raid or emigration columns sometimes attracts additional majors to the area. This has been most useful with *E. mexicanum*, *L. praedator*, and *L. coecus*. However, sometimes this technique does not work, and the ants disappear completely.

Except as indicated above, I have not been able to find a method for selectively collecting workers of certain sizes. However, since the largest workers spin cocoons first, one can collect major and submajor cocoons in spinning clusters and later collect cocoons of decreasing sizes down to the minors which are the last to spin. Similarly, one can sometimes find clusters of cocoons in bivouacs on the last statary or first nomadic days. These will be the smallest workers which emerge last.

If one wishes to collect a large sample of callow workers, this is best done from the bivouac or emigration columns of the first or second nomadic days. The callows take practically no part in the raids during the first days of the nomadic phase. On the first nomadic days one can sometimes collect callows almost exclusively during the middle and latter parts of an emigration. (Additional information on collecting from emigration columns is given under the section on Collecting Queens.)

Sexual broods may be more difficult to find and to distinguish from booty within bivouacs than worker broods because of the smaller number of male and queen larvae. The immature reproductives and alate males are often scattered throughout the bivouac, and the large isolated larvae and cocoons can be easily confused with booty.

By using lights to attract males, an additional method of collecting army ant workers was discovered. On several occasions subterranean colonies of *Labidus* and *Neivamyrmex* were found attacking the insects which dropped below the light boards. The ants did not run up the walls or cloths behind the lights to attack the insects resting there, but they killed many insects on the ground below the lights. Most of the raiding activity took place in grass, possibly because the lights repelled the ants in more open areas. The ants remained in these areas for at least three and sometimes as long as ten hours, whereas without the abundant source of prey, the colonies would have shifted their raiding to other sites. These

ants could be most readily collected in large numbers by holding insect prey in the midst of the ants. When a tettigoniid was held at the tip of forceps, the ants would attack it on all sides, and vibrating or shaking the forceps often increased the number of ants that would bite the insect. In addition, more of the largest workers would join the attack. When the insect was largely covered with ants, it could be transferred to a bottle of alcohol. This method worked better than using an aspirator, since the latter would not both attract and keep more of the larger individuals in the vicinity.

Wheeler discovered that *Labidus coecus* could be attracted and trapped in great numbers by burying a few walnut or pecan kernels in the lawns near Austin, Texas (Wheeler, 1910: 264). This species will also eat roasted peanuts, but my attempts to attract *coecus* to these nuts on Barro Colorado Island were successful on only one of four attempts when the nutmeats were put next to raiding columns. Other species of army ants including *Labidus praedator* showed no attraction to dried or roasted peanuts, walnuts, pecans, or almonds. In Costa Rica hundreds of workers of *Labidus coecus* were trapped in lard when they apparently tried to feed on it (C. W. Palmer, in letter).

Estimating the Size of Colonies and Broods

There are two main methods for estimating the size of colonies of army ants. These are based (1) upon counting a fraction of the colony or (2) measuring the time required for a counted number of ants to pass a given point on an emigration. Both methods are subject to considerable error.

Since it was impractical to preserve whole colonies, which may have a volume of over three gallons of tightly packed ants, counts were made from small samples. This method required making an estimate of the proportion of the colony which was included in the sample. Since bivouacs are seldom symmetrical and normally are highly irregular in shape with indefinite amounts of vegetation, parts of logs, etc., inside of the masses, these estimates are highly inaccurate. In addition, most samples were taken when large numbers of workers were raiding or when part of the colony had emigrated. Most of my "large" samples range from 200 to 300 ml. of loosely packed workers preserved in alcohol. Such a sample is probably about 1/50 to 1/100 of a *hamatum* colony. Samples were subdivided into volumes of about 100 ml. using a 250 ml. graduated cylinder with an inside diameter of 35 mm. The preserving fluid was drained from the ants and the workers packed tightly by

tamping them repeatedly with a glass rod as they were placed in the graduate. All workers and immature stages were counted except for large samples of eggs or the youngest larvae which were estimated. The presence of a few thousand eggs or young larvae in the samples appears to make no appreciable difference in the counts of workers because the brood fits into the interstices among the workers. Both etherized and preserved volumetric samples contained approximately the same number of workers if the workers were sufficiently anesthetized to prevent their movement.

Since broods are normally kept within the bivouac for most of the day, the entire brood could be more readily seen than all the workers. The proportion of brood actually taken can be most easily judged when the brood is youngest, since at that time it is highly concentrated and has a small volume. The older the brood, the more dispersed the larvae and pupae usually become. In many cases, the young brood can be entirely exposed in a few seconds. When the brood is old and more dispersed, one has to tear apart the complete bivouac in order to see the entire brood. Furthermore, the ants carry away and cover up the brood almost as quickly as it can be exposed.

The rate of emigration of ants was estimated by recording the number of seconds for 50 ants to pass a given point. These counts were later reduced to 25 ants, which required less time and gave results of comparable accuracy. At half hour intervals four timed counts were made in direct succession unless the traffic was fluctuating enough that more frequent counts were necessary. The mean rates were used to determine the number of ants which emigrated throughout the entire period when the column was watched. Ant traffic toward the old bivouac also was counted and subtracted from the outward traffic. Of course the large number of ants which left the bivouac throughout the day on raid columns as well as those that emigrated before counting was started could only be estimated. This was done by judging what percentage of the colony had already reached the new bivouac compared by volume with the old bivouac at the same time. In most cases about half of the ants probably were on raid columns or at the new bivouac. This method is considered more accurate for counts of the worker population than the method based on preserved samples (unless one can collect at least one fourth of a colony). However, it still is very inaccurate. It is difficult to count the ants at their maximum speed which approximates 50 ants in seven seconds. At these speeds the ants were counted in groups of five. It is difficult to

estimate the numbers of ants along the route between the bivouacs and often is impractical to make counts close to the new bivouac. In addition, one still has to estimate the volume or proportion of the ants in the two bivouacs at the time when counting is started.

Examination of Samples

Some samples of living ants were examined in Panama, after they were anesthetized with ether, in order to find myrmecophiles for additional study. The ants were kept in a battery jar or polyethylene pail and anesthetized by adding a small rag soaked with ether. Then the ants were poured out, a few hundred at a time, on a white enamel pan and examined to remove the myrmecophiles. Unanesthetized ants were also sorted, but their activity more than doubled the time required. Unfortunately, both these methods reduce the number of myrmecophiles which can be recovered from a given sample of ants compared with preserving the ants in alcohol directly at the nest. Although exact comparable data cannot be given, when a large quantity of ants was brought to the laboratory alive, myrmecophiles in the sample were frequently found dead. The transporting of the ants kept them constantly excited, and probably they attacked the myrmecophiles as well as their own brood under these conditions. Dead and injured Staphylinidae were found in these samples, and Thysanura and Phoridae were notably scarce or absent. When the ants are anesthetized in a container, many of the mites drop off the ants and stick to the moist sides of the container. It is difficult to wash them off, and many are lost. For determining the positions of mites on the ants, it is best to collect samples of 100 to 500 workers in a large container (300 ml.) and then examine each worker under a microscope individually. This technique was used with all the common species of army ants found in Panama and Kansas. However, since this method is so time-consuming, it was not used enough to find the positions of all the common mites. Some mites stay on the bodies of the ants after they are preserved, but most mites and all the myrmecophilous insects fall off.

Determining Ages of Broods and Position of Colony in Activity Cycle

The approximate age of the larvae in a sample and the position of the colony in the nomadic phase were determined by comparing the lengths of the largest larvae with those of the largest full-grown larvae. (Larvae taken when cocoon spinning had just begun were

considered full-grown.) Graphs of growth rates which are useful for determining approximate ages of broods have been published for *hamatum* worker larvae (Schneirla, 1957: 114) and reproductive larvae (Schneirla and Brown, 1952: 15). Schneirla (1961: 10) has also published a graph of the growth rates including the maximum and minimum lengths of male and worker larvae of *Neivamyrmex nigrescens*. Since the largest full-grown larvae are the same length or about one millimeter longer than the length of the adult major workers, the relative age of larvae of other species of army ants can be estimated. The lengths of the larvae were measured to the nearest 0.2 mm. using a stage grid and a stereoscopic microscope. Following the method used by Schneirla and Brown (1952: 13), separate anterior and posterior measurements were made to include the curvature of the larvae. (More accurate determination of the larval ages except for the youngest larvae can be made by measuring limb buds [Tafuri, 1955]). For representative brood samples, measurements were made of the ten largest and the ten smallest larvae which were selected by eye from a petri dish. All samples had previously been examined and divided into separate vials of workers and larvae. When samples were small, each entire sample was examined to pick out 20 for measuring; when samples were large, larvae from different parts of each sample were put in the petri dish until the bottom of the dish was covered. Larvae must be selected from different parts of the sample, because they settle out according to size. Where eggs and larvae were found in the same sample, the eggs and not the smallest larvae were measured. Where larvae and cocoons were found in the same sample, the ten smallest larvae and the ten biggest prepupae or biggest larvae in cocoons were measured. Prepupae can be distinguished from larvae without opening the cocoons by the presence of a fecal pellet in the narrower posterior end of each cocoon. Within the cocoons prepupae can be distinguished from pupae by their shape. If only cocoons were found, the ten smallest enclosed larvae or prepupae and the ten largest pupae were measured. In addition, the pupae were divided into four age classes: (1) with short leg buds; (2) white, with legs expanded; (3) slightly pigmented; and (4) dark, *i. e.*, about the same as the color of emerged callows for the species.

Colony Designations and Marked Queens

Colonies studied by Schneirla or his associates are designated by the symbols he used. Included are all colonies which I observed in 1952 and 1955. Typical designations would be '48 B-II or '46

H-B. The numbers '48 and '46 usually refer to the year when the colony was first found. However, colony '48 B-II, for example, was studied only during 1947 and was designated '48 because most of the work during that trip to Panama was during 1948. All colonies which I have studied since April 1955 have been designated with the letter "E" and numbered in chronological order starting with E-101 regardless of species or locality. A complete list of these colonies is given by Rettenmeyer (1961a: 567-581). Colonies studied by other persons or samples received from different collectors have been given colony numbers prefixed by "D" starting with D-101. Queens are referred to by their colony designations.

In order to be certain that observations over a period of time concern a single colony, two methods have been used. One is to mark the queen for subsequent recognition with slits or notches cut in the abdominal terga with iridectomy scissors (Schneirla and Brown, 1950: 274). The edges of the cuts darken, and the queen can be identified by these slits if she is found again in a few days or after several years. The usual procedure, however, has been to follow every emigration in order to avoid losing a colony. These emigrations must be followed completely, as shown by several cases in which a second colony near by with almost identical brood was accidentally mistaken for a colony which had been followed on previous days. Whether a colony is the same as another colony found one or a few days earlier, can be determined by removing the queen. After several hours some of the workers will run along the previous emigration routes and some of the earlier raiding trails. They should be found at the preceding two or three bivouacs of a colony within about a day. This technique is not recommended if a colony has a sexual brood, because the colony may not accept their queen when she is returned, as reported by Schneirla and Brown (1950: 330-331). The queen should not be kept away from her colony any longer than necessary, since queens even when kept with food and several workers may die within one or two days. Furthermore, after a few days the colony may combine with a second colony of the same species. How soon this may happen is unclear because few cases have been reported. Schneirla and Rosenblatt (1961: 229) have reported that if a colony "has been without its queen for as little as 12 to 20 hours, the workers intermingle readily with those of a colony of the same species when its columns are encountered, instead of becoming disturbed and remaining apart as normally occurs." When a queen is removed from a colony of *E. burchelli* or *hamatum* with larval brood, back-

tracking columns are active for 24 hours a day without appreciable interruption. These columns are most likely to follow the previous emigration route during the first few days after their queen has been taken, and thereafter the columns seem to deviate more from the previous trails. Although a similar reaction has been seen with other species, the columns may be present only for a few hours; they may be restricted to inconvenient hours between 8:00 p. m. and 7:00 a. m.; and they may not follow the exact emigration route used earlier. Backtracking may be variable or may not occur among statary colonies and subterranean species of army ants.

Collecting Queens

One should not collect queens of army ants unless they are needed for research. Removing the queen from a colony usually destroys the colony by causing it to fuse with another colony. Before and during fusion considerable mortality of adult workers probably occurs, and the brood of the queenless colony is ultimately eaten. Because army ants are such effective predators, destroying their colonies is unwise from a practical human standpoint.

Queens running in emigration columns can be easily picked up with forceps. However, sometimes the column must be watched continuously for several hours and possibly more than eight hours before the queen passes. There is always the possibility the queen emigrated before observations were started, and she may be overlooked even if the whole emigration is watched. The best observation points for finding the queen and myrmecophiles are long logs or open clear areas of rock or soil. In these places the queen is most easily seen, and there are fewer places where the queen can hide in case she is dropped or missed in the first attempt to pick her up. If there are no workers, or only a few workers riding on the queen, she can be picked up with practically no disturbance of the column. There may be a slight ripple of excited workers running in both directions from the point where the queen was taken. This excitement disappears in a few seconds, and the ants complete the emigration. Backtracking probably starts within a few hours unless the queen is taken from the colony at night or during the emigration. In the latter cases, backtracking probably starts at dawn when raiding begins. If a minimal amount of disturbance of the entire colony is desired, taking the queen on an emigration is the best method.

The queens normally leave the old bivouacs after 50% and usually after 75% to 90% of the ants have left, although the queen of *Nei-*

vamyrmex nigrescens may emigrate somewhat earlier according to Schneirla (1958: 245). One would expect that the time when a queen of any subterranean army ant colony leaves the bivouac may be more variable than the time for a queen of an epigaeic species, since the hypogaeic bivouacs are irregular in shape and the queen sometimes may be located near the side of the bivouac where the emigration column starts. The *burchelli* queen usually leaves the old bivouac between 8:00 p. m. and 11:00 p. m., and the *hamatum* queen usually leaves the old bivouac between 6:00 p. m. and 8:00 p. m. (see table 3). However, an emigration occasionally is interrupted, and she may not leave until the next morning. Other species may start emigrations in the early morning, and the queen may not emigrate if she remains too long in the old bivouac. In these cases the emigration will be completed on the following evening, and the queen may appear early in the column. For this reason, when one watches an emigration of one of the more subterranean species of army ants, one cannot be sure he is seeing the whole emigration even if a transition from raid to emigration column is observed.

While watching an emigration, one can usually tell that the queen is approaching the observation point by an increase in the excitement of the workers. More majors appear in the column, and more workers of all sizes run back towards the old bivouac. Many workers may run short distances and then turn and run in the opposite direction along the column. The column frequently becomes wider, and more "guard" workers stand along the edges.

If the queen is dropped when one attempts to pick her out of the column, or if she is stopped by an obstruction or break in the emigration column, a section of the column may continue to be excited for over an hour. The workers may climb on top of the queen forming a pile of workers over five centimeters high. It is impossible to predict when the queen might pull out of such a cluster and continue along the emigration route. After she proceeds along the route, the excited workers may stay in the cluster and along the column near it for at least half an hour. The behavior of these workers may cause an observer to conclude incorrectly that the queen is still within the cluster.

For the above reasons, when one wishes to collect myrmecophiles continuously in the column and also take the queen, it is advisable to try to find a stretch of emigration route which is exposed for at least five meters. One can start collecting at the end of such a section away from the old bivouac. As ants and inquilines are col-

lected, the column invariably becomes disturbed to some extent. Then the observation and collecting point can be slowly moved toward the old bivouac. The ants which are disturbed apparently deposit some chemical which excites other ants as they reach the section of the trail where the disturbance took place. If the queen comes to such an area, either the chemical itself or the workers excited by the chemical may cause her to stop. Collecting from an emigration column near the old bivouac may prolong the emigration time for the entire colony by keeping the ants more excited and causing more of them to return to the old bivouac.

When collecting at one point along an emigration route, one should check at frequent intervals to see whether the ants have started a bypass or alternate route. It is possible that this type of alternate emigration route may occur among the more subterranean species with one route completely underground.

The queen and some myrmecophiles are more sensitive to disturbances of any kind than the workers. Therefore, lights should be dim and not directed on the queen or myrmecophiles any more than is necessary. It is better to shine a light on the column from an angle so that it strikes the ants somewhat posteriorly rather than head-on. No accurate measurements of the intensity of lights used were made. However, standard flashlights with two cells were too strong when the batteries were fresh. About one third to one half this intensity worked better. When fresh batteries were used, putting a piece of medium to dark red glass or plastic over the light gave a light which seemed to disturb the ants less. The most useful type of light has a separate battery pack connected by wires to the light which can be worn on one's head. The light is easily directed and both hands are free for other purposes.

Collecting Males

Males collected in emigration columns almost invariably have workers riding or clinging to them. These workers should be pulled off the males before the males are put into alcohol in order to make it possible to determine the numbers and kinds of myrmecophiles riding on the males. Ideally, each male should be put in a separate vial and examined alive to determine the exact position of the myrmecophiles. Since this is often impractical, the easiest technique to use in the field is to isolate the males from brood and workers.

The males of most species of army ants have been taken only at

lights. At some times of the year in certain localities, it may be possible to collect over a hundred males of a single species on one or a few nights. However, a flight of this type may not be observed again in the same locality for a year or several years. Since it is impossible to predict exactly when a large flight will occur, it is best to run lights nightly. Most flights of army ants in Central America take place during the dry season and early rainy season. In the United States they may occur from early April to November. There is inconclusive evidence that some males fly to lights only between midnight and 6:00 a. m. which may indicate that these species emigrate at this time. All male army ants are slow fliers with no ability to maneuver to escape predators or an insect net. Since they also are incapable of stinging and have a completely ineffectual bite, they can be readily picked off windows or light boards.

Males taken at lights should also be examined alive with a microscope or put individually in vials of 70% alcohol. Several species of myrmecophilous mites are known to ride on the males during flight. These and perhaps other species of mites or myrmecophilous insects may fall off the males in alcohol or if the males are put in dry killing bottles. If it is not practical to put each male in a separate vial, they should be separated into vials according to species. In most cases the males seen at light can be readily separated into species by the shape and color of the head, mandibles and abdomen.

During 1952 and 1955 between one and four 50- to 100-watt incandescent light bulbs outside the old laboratory building on Barro Colorado Island were checked almost nightly for males. The windows of the Chapman House were also frequently checked, and occasionally a "Coleman" gasoline lantern was used in the forest or at the new laboratory building for attracting insects. During 1956 a greater effort was made to check the lights several times each night. On almost every night lights were used outside the north, south and west walls of the old laboratory and the west wall of the new laboratory. At each locality an incandescent bulb of 100 to 150 watts was placed in front of a white wall or cloth. Reflector flood bulbs of 150 watts directed toward the forest with a 100-watt bulb near the white background provided the best combination for attracting the maximum number of insects. Army ant males occurred in such irregular numbers that it was impossible to determine which combination of lights might be most effective. However,

there was no indication that a stronger light repelled the army ants. Ultra-violet lights also attract male army ants, and probably these lights would have given better results. On a number of nights, as many as seven army ant males were taken at the light at the new laboratory, when they were not taken at the old laboratory. On other nights, one or two males were taken at the south side of the old laboratory, but none at the west or north sides. Other males were taken when they were attracted to a "Coleman" kerosene lantern or to a headlight in the forest. Thus, a number of lights is strongly recommended for collecting males even if the lights cannot be distributed over a wide area. The finding of several colonies of subterranean species of army ants raiding the insects below the light boards was an unexpected result of the use of these lights.

Collecting Myrmecophiles

Myrmecophiles were usually collected by aspirating them from clusters, refuse deposits, or ant columns. Sometimes they were found by sorting through large samples of living or dead ants. The general suggestions which were given above for collecting workers and queens along emigration columns also apply to collecting myrmecophiles. Any disturbance of the column makes it much more difficult to collect myrmecophiles. Myrmecophilous beetles and Thysanura coming to a disturbed section become highly excited. They run faster and in a devious route and hide frequently under leaves or other objects along the emigration trail or a few centimeters away from it.

Forceps should never be used for picking up any of the myrmecophiles with the possible exception of species with hard, rigid bodies, such as histerids and millipedes. All others not only are usually killed or severely injured by attempts at picking them up with forceps, but also they are frequently damaged so badly that they cannot be determined. The simple aspirator described by Borgmeier (1958b: 290) seems to be the most efficient for collecting even highly fragile insects like phorids and Thysanura. The modification that I have found useful consists of a straight glass tube about 8 mm. in diameter and 75 mm. long. One end is covered with a piece of fine nylon gauze, and this end is inserted into a piece of rubber tubing about two feet long which holds the gauze in place. The gauze should be large enough that it can be shifted to a clean area when the spot over the tubing gets covered with dirt. An aspirator of this size works well for all myrmecophiles

and all but the largest workers. The largest major workers can be picked up with this size aspirator, but more suction must be used, and they may become wedged in the tubing. Therefore, forceps are more suitable for the largest majors. It is important to be able to quickly take the aspirator apart to remove insects which sometimes cling to the gauze by their legs or mandibles. Most specimens will drop out of the tube unless constant weak suction is used or a finger put over the end. Thus, they can be readily transferred to vials or laboratory nests. Aspirators also were useful for collecting flies and other arthropods in and around refuse deposits and over swarm raids. The arthropods in the refuse deposits were sampled primarily by using Berlese funnels.

Straight glass tubes the same size as the one used for the aspirator make excellent containers for living myrmecophiles. A number of these tubes can be placed upright in a dish of plaster of Paris in order to fill one end with a plug of plaster about two centimeters long. When the plaster has started to set, the tubes are removed from the dish, and the excess is wiped off the outside of the tubes. Before using, the tubes are placed in water to saturate the plaster, and then the opposite end is plugged with cotton. In these vials the humidity is close to 100%, which is desirable for all species of myrmecophiles and army ants.

Myrmecophilous Histeridae and Staphylinidae have been taken by others at lights, but I have never been successful at finding any at lights in Panama or Kansas.

When watching living ants in order to collect myrmecophiles, one can easily see most of the largest insects riding on the ants. As an aid for recognizing the smaller arthropods, a list of the places where these arthropods have been seen riding is given here. The families or groups which are found on the respective parts of the ants are given in parentheses. All the insects and the larger mites on ants running in emigration columns can be seen even at night using dim red light. The smallest mites can be seen only with some magnification. Although some of these myrmecophiles have also been found in comparable positions on males or queens, the following positions refer to workers unless another caste is stated: (1) riding or being carried under heads (Histeridae); (2) under petioles or gasters (Histeridae); (3) dorsal or dorsolateral parts of heads, often giving heads an asymmetrical appearance (Histeridae, circocyllibanid mites); (4) middorsal regions of alitrunk and gaster (mites, Histeridae, Staphylinidae and Limulodidae);

(5) mandibles of major workers, appearing like a large lump (Circocyllibanidae); (6) tarsi of larger workers, appearing swollen or to have dirt stuck to them (macrochelid mites, Limulodidae); (7) undersides of tibiae, appearing to have a lobe or swelling (planodiscid mites); (8) antennae, especially the scape, appearing to have a lobe or swelling (uropodine mites); (9) any part of body of adults, larvae, or booty appearing as small light or dark spots or lumps (Limulodidae, mites); (10) under heads next to bases of mandibles (neoparasitid mites); (11) under front coxae (scutacarid and pyemotid mites); (12) venter between coxae (Scutacaridae and Pyemotidae); and (13) external genitalia of males (laelaptid mites). Many myrmecophilous insects, including some as small as about one millimeter long, run in the ant column. No mites were seen to run in the ant columns during this study.

Laboratory Nests

Large samples of living ants were usually collected in three-gallon polyethylene pails and then transferred to laboratory nests. By attaching a tube to a hole cut in the plastic pail and then turning on a 50-watt incandescent light close to the pail, the ants would gradually run through the tube into another container. "Tygon" (modified vinyl plastic) tubing, formulation S22-1, with an outside diameter of one-half inch and a 1/16-inch wall was used. This tubing is translucent allowing one to see the position and size of the ants. "Tygon" formulation B44-3 probably would be superior, because it is more transparent. The combination of heat and light would usually drive the ants out of a pail in four to 24 hours. A supply of water (and booty if available) was put in a dark receiving nest. Three general types of laboratory nests were used; all are modifications of those used by Schneirla.

A vertical nest shown in figure 4 was used to keep large groups of over 20,000 workers. The main vertical sides of this nest were two sheets of glass about 26 by 40 cm. held against a wood frame. The two sheets of glass were about 25 mm. apart and rested on a foam rubber gasket cemented to the wood frame. The glass was held tightly against the gasket along each edge by wooden blocks fastened by bolts and wing nuts. These removable blocks allowed the glass to be slid off the nest from any side, or the nest could be turned horizontally, and the glass lifted vertically. Approximately half the area of the top, bottom and edges was made of wood, and the remaining area was brass screening with 78 meshes per 25 mm.

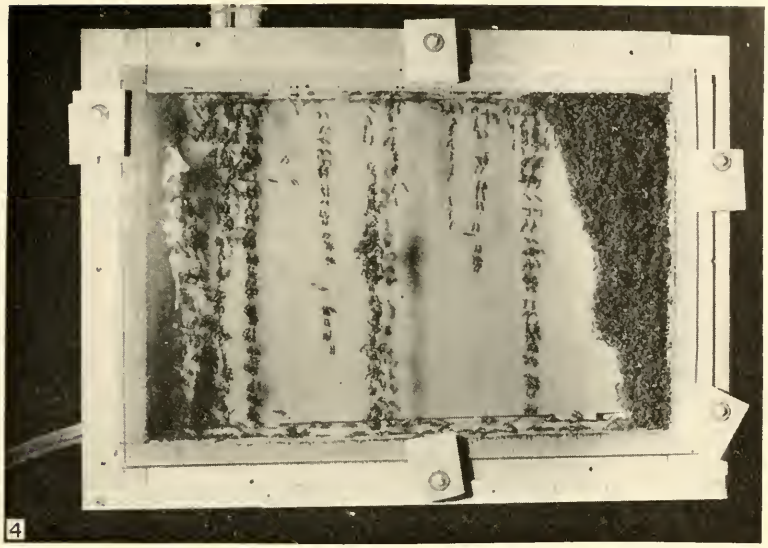


FIGURE 4.—Vertical laboratory nest with "ropes" of *Eciton hamatum* and large cluster of these ants hanging at right side. Water is supplied by capillary action from bottle by three 5 mm. diameter cotton cords seen at top left. Entrance tubing about 12 mm. in diameter is at lower left. Glass front and back are held tightly against foam rubber strips by wood blocks bolted to wood frame of nest. Light gray paper is behind nest.

Several strands of rope extended from a water bottle through a hole in the top of the nest to supply water to the ants. No food was placed directly in the nest. The ants were fed by placing food in other horizontal nests and connecting these to the vertical nest by the "Tygon" tubing.

This vertical nest worked well for holding large numbers of ants and was useful for observing the formation of strings or ropes of ants building up to a large cluster like their bivouacs. However, this nest was practically useless for observations on myrmecophiles. When myrmecophilous mites or insects were seen in the nest, they usually became lost immediately as they ran among the ants. Observations on the feeding of ants and myrmecophiles were made in horizontal nests or chambers ranging in size from about 35 by 45 cm. down to small cells about five by ten millimeters. The largest horizontal nests were wood frames with sponge rubber along the edges. A piece of glass rested on the rubber strip as in the vertical nest, but only the weight of the glass held it in place. Since the ants had some difficulty running on glass, the bottom pane of glass was covered with a sheet of paper. The largest nests were used in at-

tempts to get observations on the ants raiding and killing insects in the laboratory, as well as observations on the flies accompanying the ant raids. These nests were also useful for observing circular columns as shown in figure 22. Columns of this kind were used to observe how myrmecophiles emigrate, since these columns reproduce many of the essential features of the ant emigrations.

Some smaller nests, varying from 15 by 15 cm. to 25 by 30 cm., were made with pieces of cloth for the bottom instead of glass. The cloth was stretched tightly and held to the wood by U-shaped wire staples from an ordinary paper stapler. When cloth was stretched tightly, the ants could not readily bite it or pull holes in it. Each nest was placed over a board so that half of its area overlapped the board. On the board was a second cloth with one end in a dish of water. Water would soak through the lower cloth and keep the one attached to the nest moist and the humidity high in the nest. Air could pass through the half of the nest not touching the board with the wet cloth. A small piece of wood under the edge away from the board kept the nest from tipping.

For most observations on the behavior of any of the arthropods, petri dishes were found to be convenient. These had a small enough area that the entire dish could be placed on the stage of a microscope. They also lack corners in which many of the guests could hide. Filter paper in the bottom was kept moist in order to keep the humidity high and to hold the paper tightly against the bottom of the dish.

Since almost all the myrmecophilous insects move rapidly, it was usually impossible to observe them alive under a microscope. To alleviate this problem, small cells were molded or cut in plaster of Paris or paraffin blocks. These cells varied from 24 by 36 mm. down to five by ten millimeters in size. Microscope slides were used as covers for these cells. Glass tubing the same diameter as the aspirator was used for an entrance to these cells. A myrmecophile could be introduced into the tube using the aspirator, and a glass rod pushed down the tube would force the specimen into the cell. Although these cells were convenient for observing myrmecophiles with a microscope or for taking photographs, the arthropods usually would not feed or carry on other normal activities in the cells.

A passageway which had both a top and one vertical side of glass was most practical for observing and photographing columns of ants and myrmecophiles laterally. This passageway was about 30 cm. long, 1.5 cm. wide, and 2.0 cm. high. The base, ends, and second

vertical side were of wood with holes in opposite ends for connecting tubing to ant nests.

All laboratory nests and containers used for observations and rearing attempts were kept in laboratories with no temperature control (Chapman House or the new large laboratory building). The temperature fluctuated between 25° and 31°C. and was usually several degrees higher than forest floor temperatures or soil temperatures where these arthropods live. Weber (1959: 154) reported a range of 25.7° to 27.8°C. for temperatures of shaded soil from the surface to a depth of 30 cm. Moist filter paper, cloth or cotton in or on all nests and dishes usually kept the relative humidity high. The petri dishes and small chambers or vials used were too small for humidity measurements with the equipment available.

Photographs

All photographs were made with a Kine Exakta VX with 50 mm. Zeiss Tessar f. 3.5, 58 mm. Meyer Optik Primoplan f. 1.9, or 135 mm. Zeiss Triotar f. 4 lenses. A few were taken with the latter lens on a Praktica camera. Extension tubes and bellows were used for various extensions up to about 400 mm. The films used were Panotomic-X, Plus-X, or Daylight Kodachrome. Copies of the colored slides were made on Panatomic-X sheet film using an enlarger. A few pictures were made with Daylight Ektachrome. Plux-X and Daylight Kodachrome have given the best results. Every picture used for the figures was made with an electronic flash having a flash duration of about 1/1,000 second. A flash with a shorter flash duration would be preferable because the ants and myrmecophiles moved so quickly that some blurring occurred. Moreover, the flash frequently caused the workers, queens, and myrmecophiles to turn and run away, whereas one with a shorter flash duration might be expected to have less effect.

The Exakta was also found to be extremely useful for observing the ants both in the laboratory and in the field. A penta prism viewfinder was used with the normal ground glass replaced with a clear glass. Then the camera could be used as a wide field microscope with a great range of magnification and an exceptionally bright image. The camera mounted on an elevator tripod was much more adaptable than a microscope for viewing at any angle and rapidly switching from horizontal to vertical viewing.

OUTLINE OF THE TAXONOMY OF THE ARMY ANTS

The ants or Formicidae are usually divided into six to nine subfamilies; one of these, the Dorylinae, includes all the ants commonly referred to as army ants. Although a few other ants have some of the habits of the Dorylinae, none so far as is known possesses all the behavioral characteristics of this subfamily (see Introduction). Wilson (1958) discusses similar habits among ants in other subfamilies.

The Dorylinae are primarily found in tropical areas of the world, and most species are restricted to areas of humid tropical forests. For many years the subfamily has been considered composed of two distinct groups: the Old and New World species. The latest revision by Borgmeier (1955) divides each of these two groups into two tribes: the Dorylini and Aenictini of the Eastern Hemisphere and the Cheliomyrmicini and Ecitonini of the Western Hemisphere. Information on the biology of the dorylines of the Eastern Hemisphere is limited primarily to *Dorylus* (*Anomma*) [see Wheeler (1910), Raignier and Van Boven (1955), Raignier (1959), and Schneirla (1957b)].

Of the two Neotropical tribes of army ants, the Cheliomyrmicini is rarely seen and almost nothing is known about the habits of its species. Only a single genus, *Cheliomyrmex*, with five species, is included in the tribe (Borgmeier, 1955: 58-76).

The Ecitonini includes 135 species distributed among four genera as follows: *Eciton* (12 species), *Labidus* (8), *Nomamyrmex* (2), and *Neivamyrmex* (115). About half of these species are known only from the male caste. In some cases the males and workers must have been described under separate names, but at present it is impossible to decide which species are synonyms because the castes have not yet been found together in the same colony. There are approximately 25 more species of males described than workers, indicating that subterranean workers of at least this many species remain to be discovered. Ways to recognize the Ecitonini in the field are given above under methods, along with a key to the more common Panamanian species. Complete keys and descriptions of all species of Neotropical dorylines are given by Borgmeier (1955).

Based on the morphology of the ants, Borgmeier (1955: 137) considered *Labidus* to be the most primitive ecitonine and *Nomamyrmex* intermediate between *Labidus* and *Eciton*. However, after the first queen of *Nomamyrmex* was found, he thought *Nomamyrmex* might be more primitive than *Labidus* or *Eciton*

(Borgmeier, 1958a: 201). *Neivamyrmex* was considered to be closer to *Labidus* than to the other genera. The morphological evidence seems to link *Nomamyrmex* and *Labidus* more closely together than any other genera. It seems clear that *Eciton* is the most highly specialized of the four genera.

Borgmeier (1955: 173) has divided the species of *Eciton* into several groups based on morphological comparisons of all castes. The first of these groups includes *E. burchelli* (Westwood), *quadriglume* (Haliday), and *dulcius* Forel. *E. dulcius* is apparently not considered to be as close to *vagans* (Olivier) as it is to *quadriglume*. *E. vagans*, however, is also considered close to *quadriglume* (*t. c.*, p. 232). On the basis of the workers, *dulcius* and *vagans* appear to me to be one of the most closely related pairs of species. *E. hamatum* (Fabricius) and *drepanophorum* F. Smith are placed in a second species group. These two species are surely closely related, but *hamatum* and *burchelli* are also closely related based on the workers. *E. vagans* and *mexicanum* Roger are placed in a third group. This seems reasonable; however, I think *dulcius* may be more closely related to *vagans* than to *mexicanum*. Borgmeier (1955: 173) places *lucanoides* Emery in a separate group presumably mainly because of the thickened tarsi of the queen and a tooth on each mandible of the major workers. This latter character may not be of such great importance, since Borgmeier (1955: 263) states that a weaker tooth is found sometimes in *vagans* and *quadriglume*. In addition, I have found a small percentage of *hamatum* majors with distinct teeth on their mandibles. Apparently all majors of *lucanoides* have these teeth, although only three specimens of *lucanoides s. str.*, and an unstated number of *E. l. conquistador* Weber were examined by Borgmeier (1955: 263, 265). On the basis of the workers and queens, *lucanoides* may be quite closely related to *hamatum*. The differences in the petiolar spine of the workers as given by Borgmeier (1955: pl. 12, figs. 1, 6) are not reliable for all specimens. Unfortunately, the male of *lucanoides* is unknown. However, the queens of *hamatum* and *lucanoides* are also among the most similar *Eciton* queens, judging from Borgmeier (1955, 1958a).

Of the eight species of *Labidus*, four are known only from the males. Two, *spininodis* (Emery) and *mars* (Forel), are extremely rare, and no myrmecophiles have been reported from them. The remaining two species, *praedator* (F. Smith) and *coecus* (Latreille), are among the most common species of Ecitonini and have the largest geographical ranges. *L. coecus* ranges from Louisiana, Okla-

homa, and Texas to northern Argentina, whereas *praedator* is restricted to more humid areas. *L. praedator* and *coecus* are considered closely related among the species in the genus (Borgmeier, 1955: 83).

The genus *Nomamyrmex* includes only two species, *esenbecki* (Westwood) and *hartigi* (Westwood). The former ranges from Texas to Argentina. *Noma. hartigi* is rarer than *esenbecki*, and although both species are known from Panama, only *esenbecki* has been found on Barro Colorado Island.

Neivamyrmex includes 115 species of which 58 are known only from males and 36 only from workers. Borgmeier (1955: 286-289) has arranged all the species into groups, but only the species considered in this paper will be mentioned. *Neiv. legionis* (F. Smith), *pseudops* (Forel), and *gibbatus* Borgmeier are in group II. *Neiv. pilosus* (F. Smith), *postcarinatus* Borgmeier, and *humilis* (Borgmeier) are in group III. *Neiv. sumichrasti* (Norton), *nigrescens* (Cresson), *opacithorax* (Emery), and *harrisi* (Haldeman) are in group IV. Among these species, *opacithorax* and *nigrescens* are considered closely related. The range of *nigrescens* is apparently included within that of *opacithorax*.

Borgmeier has divided some species of army ants into subspecies or races on the basis of morphology and color. A number of these subspecies are based on collections from one or only a few colonies. Moreover, some of the characters used to separate these subspecies are of doubtful value, and some of the subspecies appear to be sympatric. In spite of these shortcomings, these subspecies in most cases are useful categories for discussion of the geographical distribution of the ants and myrmecophiles.

BIOLOGY AND BEHAVIOR OF ARMY ANTS

Eciton hamatum (Fabricius)

E. hamatum (Fabricius) can be considered one of the more specialized, and thus, less typical species of Ecitonini. However, since it is also the species which has been most studied, it is convenient to discuss it first. It has been studied extensively primarily because: (1) its behavior shows marked contrasts with that of *E. burchelli;* (2) it is common on Barro Colorado Island (and many other areas of humid lowland tropical forest); (3) its nests are usually epigaeic, that is, above the surface of the ground rather than subterranean; and (4) its much milder sting and smaller colonies make it easier to work with than *E. burchelli*, the second common epigaeic species. It should be emphasized that the term epigaeic

as used in this paper is a relative one. The species of army ants can be arranged in a sequence from the most epigaeic species to the most subterranean or hypogaeic species. The most epigaeic ones nest, raid, and emigrate on or above the surface of the ground. In addition, their columns are more frequently found during the day, including days during the dry season and sunny days. The terms subterranean and hypogaeic will be used as synonyms in contrast to epigaeic. Schneirla (1958, etc.) has often followed this usage of the terms epigaeic, hypogaeic, and subterranean, but he has also used terrestrial in contrast to subterranean. Terrestrial should be preferably restricted to its more common usage as a term in contrast to arboreal, aerial, or aquatic.

Raids of *Eciton hamatum*

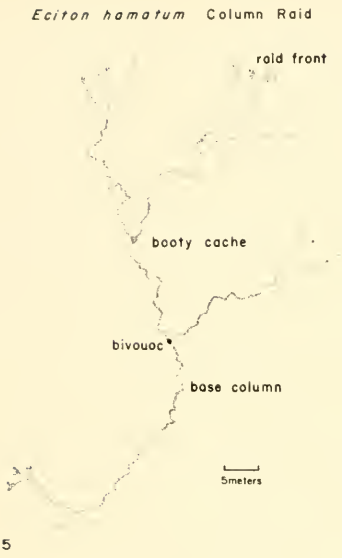
E. hamatum feeds primarily on immature stages of wasps and nondoryline ants and captures adult insects only when its raids are largest and the foragers most excitable (Schneirla, 1956b: 394). Although many species of nondoryline ants are captured by *hamatum*, it does not prey on *Paraponera clavata* (Fabricius), the largest ponerine on Barro Colorado Island. It also seems to overlook many of the smallest species of ants, and I have seen *hamatum* columns sharing the trails of *Atta* while the leafcutter ants had an active column. The two species occasionally bumped into one another, but no fighting was seen. If a raid column of one colony of army ants comes in contact with a raid column or swarm of another colony, some inconclusive fighting occurs. "Picket lines" or rows of workers of both species (or colonies) facing each other are formed along the line of contact. These workers will attack if a member of the other colony tries to cross the line, but generally there is little conflict. The ants continue their raiding by diverging away from the area of contact, or one colony may cross the other along a log or liana.

The wasps that *hamatum* attacks primarily are the social Polybiinae and Polistinae (Vespidae). Even though colonies of stingless bees are common on Barro Colorado Island, I never saw any species of army ant attack these colonies and never found Meliponinae among the booty. Schneirla (1933: 269) reported that *hamatum* kills stingless bees, but such attacks must be rare. Perhaps these bees escape because their nests or the entrances to them are made of waxes, plant sap, or mud which the ants cannot penetrate. Although on a few occasions I have seen *hamatum* raiding columns within one-half meter of stingless bee nests, the ants ignored these

nests completely. However, adjacent wasp nests were found and plundered. Perhaps the ants are aided in finding prey by odors of the wasps, by previous chemical trails of raiding army ants, or by chemicals deposited near the nest by the wasps. A colony of polybiine wasps nesting in the Haskins Library building at the Canal Zone Biological Area had its entrance through a small hole in the concrete wall about two meters above the ground. A raiding column of *hamatum* proceeded so directly to this hole and carried off the wasp brood that it appeared they were guided in some manner over the seemingly homogeneous surface of the wall.

E. hamatum and *burchelli* will run over nests of muddaubers (Sphecinae and Trypoxyloninae) without hesitating or attacking the closed mud nests. The ants were never seen on such nests when cells were open. When *hamatum* was seen attacking nests of polybiine wasps or *Polistes,* the ants pulled off the caps of cells containing pupae and completely stripped the nest of all brood. The adult wasps were killed if they stayed on the nest. Most of them retreated to adjacent vegetation where wasps returning from foraging joined them. Excellent photographs of army ants attacking nests of *Polistes* have been published by Michener and Michener (1951, fig. 89) and Klots and Klots (1959: 248). One colony of ants (E-233) made a bivouac in a hollow log that must have been the site of a polybiine nest. After the bivouac was located, many wasps were seen flying directly to the small entrance hole in the side of the log. They all stopped abruptly at the entrance, and then most of them joined clusters of wasps on neighboring vegetation. A similar case was observed when colony '52 H-I made a bivouac in a hollow tree displacing a polybiine colony. In all cases where army ants have been observed to raid nests of vespid wasps, the wasps abandoned their nests. Since this appears to be a fairly frequent occurrence, many reputed cases of vespids starting colonies by swarming may be attributable to army ant raids.

The foraging pattern of *hamatum* has been termed "column raiding" in contrast to that of *burchelli* called "swarm raiding." These two types, which have been extensively studied and described by Schneirla (1933, 1934, 1938, and 1952), are diagrammed in figures 5 and 6. While in swarm raids the advancing group of ants is a large mass or swarm, column raids have small groups of workers in narrow columns at the advancing edge or raid front. The individual workers comprising the advancing front are constantly changing. These advancing ants may fan out at the tips of the distal raid columns, but these groups are small and usually cover



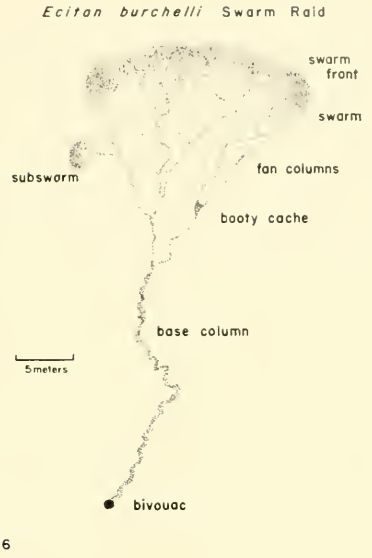


FIGURE 5.—Column raid of *Eciton hamatum*. Advancing front of raid is made up of columns or small groups of workers. Almost all army ants have similar but smaller "column raids" with one to three columns leaving the bivouac. Prey often is deposited in booty caches at junctions of columns. Base columns extend from bivouac to first forks.

FIGURE 6.—Swarm raid of *E. burchelli*. Advancing front is made up of large mass or swarm of workers. Anastomosing columns in fan area converge to base column.

no more than one or two square decimeters of surface. Since the workers do not cover a large area at one time like the swarm raiders, *hamatum* does not continually drive out large numbers of arthropods in front of its raids. As a consequence the flies and ant birds dependent upon these arthropods are absent or rarely seen. Although I have never seen ant birds near this army ant, Schneirla (1933: 268) has reported seeing them near "unusually vigorous *E. hamatum* raids."

The raiding workers of *E. hamatum* run primarily on the ground and on the surfaces of leaves. They also climb vegetation and buildings, but rarely go more than two meters above the ground. The workers will also go into subterranean nests and attack ants living in them. During the dry season they are more apt to run under leaves and other objects rather than on top of them as in the rainy season (Schneirla, 1947: 11). However, even in the dry season they make frequent use of logs, lianas, and other similar objects to cross streams and ravines and to make their raid and emigration routes shorter and smoother.

A continuous column of ants connects the advancing distal raid columns with the bivouac. When a strong raid is in progress, the base column may be one to six ants wide for more than 100 meters from the bivouac. During the hours from about 11:00 a. m. to 2:00 p. m., called the "siesta period" by Schneirla, there is a decrease in raiding activity. This decrease may be more noticeable during the dry season, and Schneirla and Brown (1950: 296) have reported that the base column may even become discontinuous during the midday hours. Although at times base columns became so weak that only a single ant could be found every one to three meters along the trail, I have never seen a raid during the dry season that did not continue to have some traffic between the bivouac and the front of the raid.

Raids of nomadic colonies of *hamatum* almost always start shortly after dawn and are presumably initiated by the increase in light intensity at the bivouac. Statary colonies which often do not start raiding in the morning may start a raid after the siesta period. Temperature effects have been considered subordinate to light for inducing these diurnal peaks in raiding activity (Schneirla, 1938: 82); however, "regular diurnal temperature variations are mainly responsible for the existence of two 'peaks' in raiding activity, one in the later part of the morning, and one in mid-afternoon." Apparently a colony will start a raid between 11:00 a. m. and 2:00 p. m. only if it is greatly disturbed, as for instance, when a large part of the bivouac is knocked down. Although it would seem that sunlight striking a bivouac might have this same effect, no records of this are known to me. All army ants are considered blind from the standpoint of seeing an image, but they do react to different intensities of light. Army ants apparently find their way back to their nests not by any visual orientation but solely by a chemical trail. When raiding, the leading ants deposit a chemical trail which is followed and added to by the subsequent workers. The trail is probably not polarized, since the ants apparently cannot tell the direction to the bivouac solely from the chemical on a short length of trail. If a stick which is part of the trail is reversed, the ants show some hesitation only where the continuity of the trail is broken at the ends, and they do not reverse their direction (Schneirla, 1933; 1944a: 5). *E. hamatum* workers can also follow the trails of *burchelli* (Schneirla, 1944a: 3) and possibly those of any species of army ants. How long these trails last and how often they are re-used is debatable. The most outstanding cases where chemical trails appear to have been re-used involve emigration trails (see

below under emigrations). On several occasions I carefully marked exact routes of raids near the laboratory on Barro Colorado Island, and subsequent raiding ants of the same species paid no attention to these when running over the same area. However, considering the number of ants following a single trail, one would expect the chemical trails of raids to be much weaker than emigration trails.

The raids appear to be largest when colonies have a "late nomadic brood," *i. e.*, a brood of larvae which is almost ready to spin cocoons. At this time a raid usually has three base columns radiating from the bivouac for 150 to 300 meters. The raids are more likely to be smaller during the early nomadic phase, and on some days in the statary phase no raids may occur. On days when there are raids in the statary phase, the traffic along the columns is one-fourth to one-half as great as on nomadic raids (Schneirla, 1957a: 109).

Although raids during the nomadic phase are larger than those in the statary phase, both in the number of base columns and in the number of ants which take part, the maximal distance from the bivouac sometimes is greater in statary raids. Since the colony is in one location for about three weeks, it can establish chemical trails for several hundred meters from the bivouac and also plunder most of the colonies of potential food near the bivouac (Schneirla, 1944c: 173). No adequate quantitative data on raid distances have been published, however.

Compared with the behavior of *hamatum* in the rainy season, in the dry season raid columns are more frequently under leaves, statary colonies are likely to have fewer raids per phase, and nomadic colonies have smaller raids (Schneirla, 1947: 11; 1949b: 74, 78). Although these contrasts appear valid, colony '46 H-B studied by Schneirla did not show an increase in raiding in a statary period during the rainy season (May to June) compared with the two preceding statary periods during the dry season (February to April). The number of raids compared with days when the colony was observed during the three statary periods are respectively: 9 out of 19, 11 out of 19, and 6 out of 13 (Schneirla, 1949b: 20-22, 74).

Emigrations of *Eciton hamatum*

At the end of the siesta period there is usually an increase in traffic moving outward along one or more raid columns. This afternoon exodus may gradually increase and result in an emigration along one route. Sometimes the early afternoon exodus decreases and a second exodus in late afternoon or early evening gradually builds up to an emigration. Schneirla (1938: 70) has stated that the ants

emigrate along the route on which most booty has been brought to the bivouac, but he has given no quantitative evidence. This outward flow may start between 2:00 and 3:00 p. m. when sunlight is still quite strong, or it may not start until after 6:00 p. m. after the light intensity has dropped considerably. Although the siesta period lull in raiding is "perhaps attributable to a combination of radiation, heat, and desiccation" (Schneirla 1956b: 400), an increase in raiding activity gradually shifting into an emigration may occur between 1:30 and 3:30 p. m. while these "detrimental" factors are still present and may even be more intense compared to 11:00 a. m. when the siesta period starts. No adequate data have been published to show any correlation between the activity of army ants and the atmospheric conditions during the siesta period. Perhaps some inherent "clock mechanism" is important for initiating these changes in raiding activity and the shift to emigration. Schneirla (1938: 83; 1944b: 453, footnotes) acknowledges the lack of direct evidence for any correlation between environmental factors and the siesta period or emigration. In addition, he considers that it is "somewhat doubtful" that a "temporal memory" or similar phenomenon produces the increase in activity in the afternoon. Ants which he kept in the laboratory under ruby glass did not exhibit any noticeable increase in activity in the afternoon at the time when colonies in the forest became more active. Schneirla (pers. com.) did not test a control nest, identical except for having colorless glass rather than dark red. However, other ants kept in the laboratory in wire nests did show some change in activity. Other tests which I ran showed no increase in activity in the afternoon; however, these may not be adequate tests of the hypothesis of a possible internal clock.

Two emigrations were seen during 1956 that were finished before 7:00 p. m. One of these occurred on 8 March 1956 when colony E-127 had completely abandoned the old bivouac site except for a strand with a width of about five ants at 6:00 p. m. The queen had left the old bivouac, and the few hundred remaining workers must have left the bivouac site by 6:15 p. m. at the latest. The second case was on 11 April 1956 when colony E-141 had a strong emigration in progress when it was visited at 3:45 p. m. Some brood was being carried at that time, and at 4:00 p. m. large amounts of brood were being carried. The queen left the old bivouac at about 6:30 p. m., and the last ants left the site at 6:50 p. m. Neither of these bivouacs had been disturbed by me during the days of these early emigrations. Normal emigrations of *hama-*

TABLE 3.—Observations of Queens of Army Ants Along Emigration Columns.

SPECIES	DATE	QUEEN	TIME	DISTANCE IN METERS FROM OLD BIVOUAC
Eciton hamatum	2 Mar. 1956	E–123	9:55 p.m.	?
	6 Mar. 1956	E–127	7:36 p.m.	10
	8 Mar. 1956	E–127	before 6:00 p.m.	0
	18 Mar. 1956	E–121	8:00 p.m.	5
	19 Mar. 1955	'55 H–E	10:06 p.m.	68
	28 Mar. 1955	'55 H–I	11:15 p.m.	15
	8 Apr. 1956	E–141	7:00 p.m.	7
	11 Apr. 1956	E–141	6:31 p.m.	6
	11 May 1956	E–159	8:05 p.m.	30
	15 May 1956	E–162	8:40 p.m.	>25
	16 May 1956	E–162	7:15 p.m.	10
	13 June 1956	E–168	7:15 p.m.	10
	23 June 1956	E–191	7:11 p.m.	5
	8 Aug. 1956	E–243	10:37 p.m.	>25
Eciton burchelli	17 Feb. 1956	E–107	8:25 p.m.	8
	23 Feb. 1956	E–107	10:15 p.m.	2
	5 Mar. 1956	E–110	11:15 p.m.	>20
	7 Mar. 1956	E–110	9:10 p.m.	100
	16 Mar. 1955	'55 B–IV–N	11:03 p.m.	90
	17 Mar. 1956	E–132	9:25 p.m.	20
	23 Mar. 1956	E–132	8:15 p.m.	22
	30 Mar. 1956	E–136	8:37 p.m.	60
	2 Apr. 1956	E–136	7:45 p.m.	25
	28 Apr. 1956	E–136	9:10 p.m.	10
	15 May 1956	E–148	8:05 p.m.	1
	26 July 1956	E–222	9:30 p.m.	20
Eciton vagans	30 May 1956	E–180	8:50 p.m.	>15
	24 July 1956	E–219	3:03 a.m.	>10
Eciton dulcius	1 Mar. 1955	'55 D–1 Mar.	9:00 p.m.	>30
	2 Apr. 1956	E–137	8:30 p.m.	> 4
	11 Apr. 1956	E–143	8:30 p.m.	>10
	4 July 1956	E–204	7:41 p.m.	>20
Eciton mexicanum	14 Feb. 1956	E–108	9:40 p.m.	> 8
	24 May 1956	E–170	10:15 p.m.	> 5
	12 Aug. 1956	E–251	9:15 p.m.	> 5
Nomamyrmex esenbecki	18 May 1956	E–164	10:28 p.m.	> 3
Neivamyrmex opacithorax	3 June 1958	E–263	12:06 a.m.	1?
	6 July 1959	E–264	11:41 p.m.	> 2

tum probably never occur much earlier than in the above cases. Schneirla (1949b: 19) reports similar times for only two out of 49 emigrations for colony '46 H-B. Large numbers of returning workers and the presence of a larval sexual brood or alate males may delay the start of an emigration and prolong it. For example, colony E-105 with a larval sexual brood started an emigration on about the third nomadic day between 8:45 and 10:00 p. m. There is no data to show that some colonies regularly emigrate earlier than others.

In eight of 14 cases shown in table 3, when the queen was seen on an emigration, she had apparently left the old bivouac between 6:30 and 8:30 p. m. By the time the queen is seen on the emigration column, 75% to over 90% of the colony has left the old bivouac judging from those cases where the old bivouac has been seen at approximately the same time as the queen.

Low light intensity may be an important requirement for the emigration of the queen and, thus, for the completion of an emigration. However, it may not be the primary triggering stimulus because emigrations can start about 3:00 p. m. Schneirla (1944c: 159) has reported that the queen is more sensitive to light than the workers. Moreover, she will turn away from a beam of light directed on her, whereas the workers "seem virtually incapable of specific orienting responses to light." This photonegative reaction of the queen is probably one of several factors which keep the queen in the central parts of the bivouac during the daytime (Schneirla, 1944c: 158-160) and would prevent or delay her emigrating during daylight. Her central position within the bivouac would also contribute directly to her late appearance along emigration columns because the lower and more peripheral ants usually emigrate first. All the ants have usually emigrated from the old bivouac by 8:00 to 11:00 p. m. However, if the emigration is delayed by heavy rains, as may be the case in the rainy season, emigrations may not be completed until after dawn the next morning. Schneirla (1944c: 160) reports two cases where queens were seen on emigrations during daylight. (These two cases must be less than 0.5% of the emigrations for which records exist but no accurate count is available.)

Emigrations with worker broods rarely show any signs of "ant roadways" or "flanges" (similar to figures 10 to 12) such as are common along emigrations of colonies with broods of nearly full-grown sexual larvae (Schneirla, 1948: 98-99). (See section on Sexual Broods and Colony Divisions.) These "roadways" are com-

posed of workers which cling to leaves or to any other objects along the path of the emigration and remain immobile while the other workers emigrate across their bodies (see figure 10). They serve a useful function, especially where the ground is uneven for any reason, since the bodies of the ants form bridges and make the path smoother. In addition, the workers form flanges at the edges of narrow lianas (figures 11 and 12) or on vertical surfaces, such as on the sides of trees. It is clear that these flanges and roadways are of considerable advantage when two or three large workers together must carry each of the larvae of reproductives which are twice the length of a single worker. The formation of these roadways, as Schneirla reports, is dependent upon workers bumping into and stepping on each other repeatedly. Near the end of the emigration when workers in the narrower column are no longer frequently stepping on the immobilized individuals at the margins of the roadway, these marginal workers are the first to move from their positions and join the emigration. Ant roadways are formed occasionally when a colony has a worker brood, but they are not as well developed. These roadways usually are close to the old bivouac where the traffic is heaviest and larvae are frequently dropped along the route. Sometimes an ant roadway will be formed for a brief distance when the queen comes to a part of the route where ants are having difficulty running. Short traces of roadways are formed occasionally along raid columns where there is exceptional activity.

"Guard workers" are frequently present but greatly scattered along the emigration columns. These are workers which face outward at the edges of the column and attack insects or other animals which may attempt to cross the column. A high proportion of these workers are majors. These guards when maximally excited keep their mandibles open wide, their antennae vibrate rapidly, and they rear upward with their front legs off the ground and their bodies almost vertical. Only workers which were not carrying booty or brood were seen to stop and act as guards. The length of time that these workers acted as guards varied from a few seconds to more than an hour for no apparent reason. In most cases, there also was no evident reason why there were guards in some places and not in others. However, any disturbance of the column results in an increase in guard workers. These guards were seen to attack beetles, sowbugs, spiders, and other arthropods which attempted to cross the emigration column. In most cases the arthropod was not killed but retreated away from the column. The same arthro-

pod that is readily killed during a swarm raid seems to have a better chance of survival when it runs into an emigration column. The ants which are laden have to be considerably disturbed before they will drop their burdens and attack. The guard workers will attack, but they seem slower and less effective than raiding workers.

When the queen approaches along an emigration column, the number of guard workers frequently but not always increases. The number of guard workers as well as the size of the "retinue," or group of workers which appears to accompany the queen, seem to depend primarily on the speed with which the queen travels. If her progress is not impeded by irregularities in the terrain, and she proceeds without hesitation, the retinue is small and there are no guard workers along the route in many places. However, if a bright light is directed at the queen and she halts, workers which are following her immediately start climbing over her and run ahead of her in a more excited manner. If she continues along the route after a brief pause, she will have a much larger contingent of workers accompanying her. These workers which make up the retinue are not the same small workers which are clustered around the queen in the bivouac. Larger workers and majors are common. The largest retinue which I have seen included between 25 and 50 majors plus a larger number of smaller workers which stayed within 15 to 30 cm. of the queen. Approximately another 100 majors were running back and forth and acting as guards as far as two meters from the queen. This queen was seen making good progress along the emigration column at a point ten to 15 meters from the old bivouac. The composition of the retinue may change to some extent as the queen progresses. The more the queen's progress is delayed, the more guard workers line the route. A similar reaction can occur if one has been collecting ants or myrmecophiles for several hours at one spot along the emigration route. The disturbed ants evidently deposit an alarm chemical which later excites the queen and other workers. Part of this reaction may be due to the "alarm" being passed from one worker to another as they reach this spot. However, on other occasions when no excited workers were noted running toward the old bivouac, subsequent workers seemed disturbed when they came to the point of observation.

Emigrations may be influenced considerably by chemical trails used previously around suitable bivouac sites by the same or different colonies. Schneirla and Brown (1950: 337) reported a colony followed an emigration route which it had used 31 days earlier. Colony '48 H-19 followed a trail more than 450 meters long made

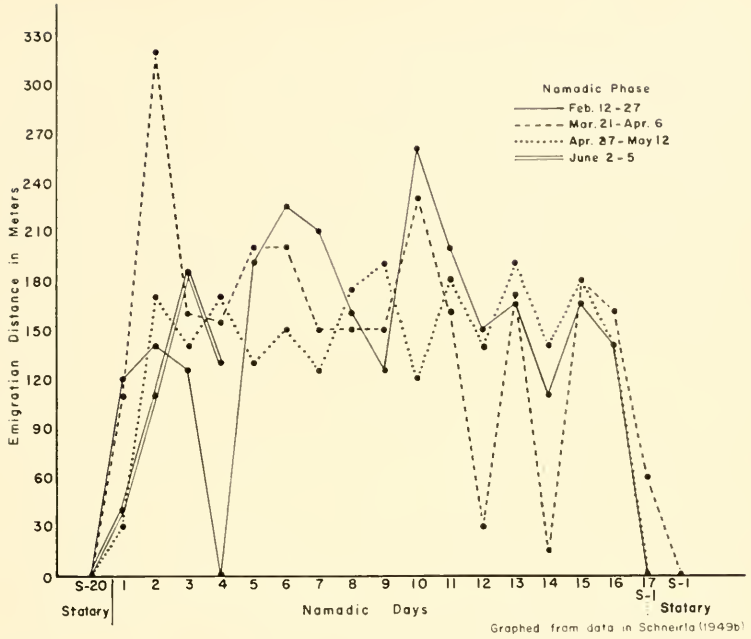


FIGURE 7.—Graph of emigration distances of colony '46 H-B, *Eciton hamatum*, throughout three complete nomadic phases and part of fourth. Distances determined by Schneirla (1949b: 17, 20-22) on Barro Colorado Island.

during the preceding week by colony '48 H-28. Another trail "approaching 40 meters in length made by colony H-15, *E. hamatum*, was employed by colony B-VIII, *E. burchelli*, after an interval of more than three weeks" (*l. c.*). These trails were also considered to last longer during the dry season than during the rainy season when more frequent wetting would be expected to wash the chemical away. Colony E-191, *hamatum*, emigrated on 19 June 1956 along what appeared for about 50 meters to be the identical route that colony E-159 of the same species had used on 11 May 1956. These two colonies also bivouacked under the same end of the same log. However, I had not marked the entire route of the previous emigration. Although it was clear that along major landmarks such as lianas and logs, the two colonies followed the identical route, in a few cases the second colony did not follow the precise route used earlier. Close to the bivouac, colony E-191 deviated and took the route that colony E-159 had used when it left that site. Since it is impossible to know how many chemical trails of army ants may be on any surface, or how frequently and recently they have been

used, it seems best to be cautious when considering such cases of ants following old trails.

Regardless of the time when an emigration starts, there is a typical sequence of events which can be recognized in almost every emigration. These events will be discussed as they most frequently occur near the old bivouac. Closer to the new bivouac a similar sequence occurs except that the direction in which booty is carried may vary more if there are many branch columns in the vicinity of the new bivouac. Furthermore, the myrmecophiles are apt to be in less distinct groups. Theoretically, one could maintain that an emigration starts when the first ant leaves the bivouac at the start of a raid. However, since all these raiding ants also may return to the bivouac, the time when the first booty is carried from the bivouac is a more accurate starting point. Often a noticeable exodus of workers occurs before booty can be seen carried away from the bivouac. In all cases that I have observed, booty is first carried in both directions during this starting period. One reason that booty appears early in the emigrations is that much of the booty collected on the day's raid is concentrated in the bivouac near the raid columns. There may be considerable confusion along the column as ants with and without booty bump into each other and often reverse their direction. Sometimes a few workers with booty even try to return to the old bivouac more than an hour after the outward flow of booty and brood has begun. During this early period, myrmecophiles also are more frequently seen going in both directions along the column.

The next most obvious stage is the appearance of the brood. This is frequently preceded by a greater exodus of workers. When the brood consists of eggs or young larvae, it is almost impossible to see it. For this reason it is often advisable to take samples from the column approximately every half hour. If these samples are put into alcohol, the brood is usually dropped by the ants and sinks to the bottom. Myrmecophiles are common during the passage of the brood; and some kinds, particularly any which feed on the brood, may be more abundant than at any other time during the emigration.

Near the end of the brood or after the end of the brood, the queen usually is seen. Following the queen there is a gradual decrease in traffic, later a more rapid decrease near the end of the emigration. After the brood and queen have passed, there may be an increase in the number of myrmecophiles in the column. Booty may still be seen during this terminal period, and in the absence of brood it may be much more conspicuous than previously. The end of the

emigration usually is quite abrupt, with ants decreasing from a column two to three ants wide to a trail without ants only five to ten meters away. The workers at the end of the column act in a manner similar to those at the beginning of a raid column, except that they are much less hesitant. They frequently run back in the direction of the old bivouac for a few centimeters and then turn and run after the rest of the column. After the last ant has passed the observation point, many more myrmecophiles may be seen following the trail. The species of myrmecophiles in this group may be different from any of those seen earlier in the emigration. Details on the species and abundance of the myrmecophiles will be given in a subsequent section.

Bivouacs of *Eciton hamatum*

The nests of army ants are called bivouacs primarily because they are much more temporary than the nests of other ants. The bivouacs are made up of the bodies of the ants which hang by their legs from some support. Detailed discussions of the formation and internal composition of bivouacs and several photographs of typical bivouacs have been published (Schneirla, 1933: 1949b; Schneirla, Brown, and Brown, 1954). The ability and tendency for the army ants to form hanging clusters seems to be unique among the ants. Other ants form piles of workers that may be many workers deep, but as far as I can determine, none will form "threads" of workers hanging together by their legs or large clusters of workers hanging from a support. Schneirla has repeatedly mentioned the "opposed recurved hooks" on the tarsi of the ants and stated or implied that these are "specific organic characteristics" necessary for forming this type of cluster (Schneirla, 1956b: 382; Schneirla, *et al.*, 1954: 293). However, most insects and probably all ants have "opposed recurved hooks." The only significant difference about the tarsal claws may be that they are slightly larger than those of most ants. They are not more recurved so far as I have observed. The tooth on the medial or lower margin of the claws is also not a necessary characteristic for this type of clustering. Other ants also have this tooth, and *Neivamyrmex* does not have it. In addition, the army ants appear to have relatively long and thick legs. Limited comparisons with ants of the same length, showed that the legs of the army ants in most cases were longer.

When the other ants had legs of equal length, the legs of the army ants, especially the tarsi, were thicker.[1]

Bivouacs are located usually under logs, in hollow logs or trees, between the buttresses of large trees, in underground cavities such as mammal burrows, in piles of brush, or similar places. Much has been written about the selection of bivouac sites, and many factors have been found to influence this selection. However, the relative importance of these factors is extremely difficult to estimate. Although the ants usually form their bivouacs in sheltered sites which are cooler and more moist than surrounding areas, the ants do not make a selection on the basis of temperature or humidity gradients. The selection is a more indirect one based primarily on the behavior of the ants and the mechanics of nest formation (Schneirla, Brown, and Brown, 1954; Jackson, 1957). Toward the end of the nomadic phase and in the statary phase, there is a distinct shift to sites which are more sheltered and thus, cooler and more moist. The choice of site and formation of bivouacs are influenced by the following factors listed without regard for their relative importance. All these factors, except numbers 9 and 12, have been considered and in most cases discussed at some length by Schneirla, Brown, and Brown (1954).

(1) Some support from which the ants can hang is apparently essential. This support also supplies some shelter. (2) Lack of disturbance by rain at the time of bivouac formation is important. If rain strikes a bivouac during formation or after it is formed, the ants may shift, depending upon the severity of the rain and the availability of a suitable site to which they can retreat. (3) Wind currents may be a crucial factor at the time of formation as well as after formation. Artificial currents will readily excite ants as they are starting a bivouac and cause breakdown of the initial ropes and clusters of ants. (4) Heat (in the absence of light) will cause ants to move their clusters in the laboratory, but it is doubtful if this ever is important in the formation of bivouacs under the even temperature conditions prevailing through forest such as that on Barro Colorado Island in the evening when emigrations occur. Bivouacs in hollow trees or logs may shift after they are formed, if sun heats the site considerably even though not striking the bivouac directly. Temperatures probably never are low enough on

1. Borgmeier (1955: 16) discovered that all Ecitonini workers (and also *Acanthostichus* and *Cylindromyrmex*) have a yellowish stripe on the undersurface of the hind tibia. This stripe varies considerably in length and width, but all workers have it. It is absent, however, on the males and queens. The stripe lacks hairs and its surface texture is different from that of the rest of the leg. Perhaps this stripe is some kind of sensory structure. Although it is not known whether this unusual character has any connection with clustering or other behavior of these ants, its significance would bear further investigation.

Barro Colorado Island to cause an adverse effect on the selection of a nest site. (5) Light similarly would not be a factor in formation of bivouacs at night, but it appears to cause shifts during the day. In the laboratory, ants will readily shift a cluster from a lighted part of a nest into a darker part. (6) Humidity normally is close to 90% at the time bivouacs are determined. Presumably if the colony nests in an area which is too dry, it will shift, if possible, to a more humid site. Colonies frequently form bivouacs at the ends of hollow logs. On the day following the emigration to these sites the colonies frequently shift deeper into the log. Humidity, light, air currents, and temperature probably all play a part in these shifts. (7) Junctions in raid columns, where opposing traffic may become confused and the outward flow blocked, may result in accumulations of workers leading up to a bivouac. If outward traffic from the old bivouac meets strong inward or "centripetal traffic" (Schneirla, *et al.*, 1954: 275), this may cause an accumulation of workers or a shift in traffic along a lateral branch column. Traffic may be drained along the lateral branch away from the initial cluster with the result that the final bivouac is formed along the lateral column. (8) Caches or deposits of booty and areas of greater booty odor result in workers stopping to feed, and the workers also drop larvae which feed on the booty. (9) Areas with considerable odor from raiding or emigration trails, as well as previous bivouacs of the same or other species of army ants may attract colonies to certain suitable sites. (10) The age of the brood or something correlated with its age probably influences the selection of the bivouac site. Colonies with more mature larval broods and pupal broods form bivouacs in more sheltered sites than colonies with young larval broods. (11) When the larvae are fully grown, the selection of a more sheltered bivouac site may be influenced by the availability of powdered rotten wood and similar detritus apparently necessary for spinning cocoons. Places where detritus of this type is more abundant typically are also more "sheltered" or "enclosed" (in the sense of Schneirla, *et al.*, 1954: 273), and the sheltering is presumably more important than the presence of detritus. (12) The presence of the queen undoubtedly has some effect on bivouac formation and its coherence or stability (compare evidence presented by Schneirla and Brown, 1950: 330-331 on queenless colonies and by Schneirla, 1953). Although a bivouac site is almost always determined and the bivouac probably over 90% completed before the queen reaches it, if the colony is divided between two sites, the part of the colony with the queen may be-

come the final bivouac. Two bivouacs may be started in nearby sites, and if the queen stops in the first one, the ants in the cluster further along the emigration route may return to the first site. Similarly, if the queen does not stop, but continues to the more distant site, the other ants are apt to follow her. Colonies deprived of their queens show varying degrees of bivouac breakdown and appear to have a weaker tendency to form a compact, undivided bivouac. (13) A bivouac will not be formed where there is a conflict with other colonies of army ants of the same or different species. Although actual fighting is rare between colonies of army ants, two normal colonies with functional queens are always to some extent antagonistic, and usually their raiding behavior would keep bivouacs apart. In a few cases where bivouacs of two colonies were observed in the same log, one colony moved out presumably because of disturbance due to the other colony. No disturbance by a nondoryline ant or other insect colony has been reported as causing a bivouac shift.

Once bivouacs are formed, major disturbances will cause shifts or complete emigrations depending in part upon the severity of the disturbance. A bivouac of either a nomadic or statary colony can be completely pulled apart and scattered around on the ground, and it usually is reconstructed on the identical site. However, if its previous support is partially or completely destroyed, the colony may move part of a meter or more than ten meters to a new site. Such a shift during the day will occur with statary as well as nomadic colonies. No shift of this type has been reported which was not due to human disturbance, but occasionally natural catastrophies such as floods, fires, etc., might cause similar shifts.

Schneirla has stated (1949b: 72), ". . . the fact that the bivouac-change processes often are more protracted and more variable in the dry months, with a greater lag in hitting upon the final bivouac site, indicates a greater scarcity than in rainy times of feasible clustering spots approximating the species optimum." No quantitative evidence was given to support this statement. However, in the same paper (p. 20-22) he gives the times when new bivouacs were started for colony '46 H-B during both dry and rainy seasons. These data show that the mean time for the starting of a bivouac was 7:05 p. m. during the dry season (dates from 12 February to 30 April), whereas it was 7:47 p. m. during the rainy season (dates from 2 May to 5 June). This also suggests that during the dry season the siesta period is not prolonged, and the emigrations may start earlier than in the rainy season. Perhaps the starting of new

bivouacs is influenced by the time of sunset which on Barro Colorado Island would be about 30 minutes later in June than in March.

Refuse Deposits of *Eciton hamatum*

As a result of the kind of booty typically collected by *hamatum* colonies, there is little refuse around their bivouacs. Even at statary bivouacs only a trace of booty could be found. Where bivouacs touched the ground or the bottom of a hollow log, there usually were a few ants walking around possibly ten to 20 cm. from the edge of the bivouac. Occasionally four or five workers would be in a weak column extending 20 to 30 cm. from a bivouac, but these columns did not end in distinct areas of refuse. One or two of these ants were sometimes seen carrying booty refuse. Some scattered refuse could often be found, composed of the more sclerotized parts of booty, such as head capsules of older pupae. Empty cocoons from booty could also be found, but they were scarce possibly because many pupae had been removed from cocoons before they were brought back to the bivouac. On the last statary day empty cocoons of the army ant brood became obvious and rapidly increased through the first nomadic day. The ants carried some of the empty cocoons a few centimeters out of the bivouac along the supports of the bivouac or along the ground if the bivouac touched it. Apparently most of the empty cocoons were dropped by workers at the edges of the bivouac. Some cocoons drifted down to the ground directly; others got caught in the sides of the bivouac and probably did not fall to the ground until the ants emigrated. As a result the cocoons were generally scattered around on all sides of the bivouac and under the bivouac as well, if the bottom of the bivouac did not rest on any support.

Often Phoridae and Staphylinidae could be seen around the edges of the bivouacs. The staphylinids probably removed most dead workers.

Size of Colonies and Broods of *Eciton hamatum*

The size of any colony of army ants is difficult to determine, and colonies of the same species must vary by more than 100% in size, in view of the method of colony formation by division. Based on counted samples of 100 ml. of packed etherized or preserved ants in which worker counts can range from about 3,000 to 6,000, I estimate that the size of *hamatum* colonies ranges from about 100,000 to 500,000 adult workers. Estimates based on emigrations probably are more accurate and tend to be somewhat lower than this.

Schneirla's largest estimate (150,000 to 250,000) (1957b: 266) must not include the maximum variation resulting from colony division.

Brood estimates vary even more widely, and it appears to me that the size of an individual brood may decrease markedly from the egg to pupal stages. Schneirla and his co-workers have emphasized that cannibalism may play an important part in the development of sexual broods (Schneirla, 1949a: 11; Schneirla and Brown, 1950: 334; 1952: 12, 29). However, in contrast to these broods of reproductives, "worker broods are produced without much evidence of cannibalism" (Schneirla, 1949a: 5). The extent of the cannibalism has not been well substantiated in sexual broods. The supposed greater extent of cannibalism when sexual broods are in colonies has been based partly on a decrease in the size of larval broods. In addition, Schneirla (1953: 36) reported that during the statary phase brood cannibalism occurs at the border of the sexual brood zone and the brood free (old queen's) zone because empty cocoons were often found along this border. Brian (1958: 500) has suggested that brood consumption may be widely connected with production of new queens in the dorylines as well as in other ants. However, I think that cannibalism of worker broods may also be extensive in colonies of *hamatum* judging from impressions of the sizes of egg and young larval broods compared with mature larval and pupal broods.

Schneirla's estimates of the size of worker broods vary from about 20,000 (1948: 109), to 40,000 (1956a: 3), to 60,000 (1957b: 266) with no indication of the age of the brood involved. One colony of "about 30,000 workers" had a "counted 32,479 cocoons" (Schneirla, 1934: 321), which would seem to be an impossibly high proportion of brood. For comparison with these estimates, Hagan (1954a, 1954c) determined that a *burchelli* queen has 2,528 to 2,644 ovarioles, each capable of producing 22 to 25 eggs per cycle. Thus, the total egg production would fall between 55,616 and 66,100 eggs during one statary period. The oöcyte number for *hamatum* was considered to be the same as in the queen of *burchelli*, but no ovariole number was determined (Hagan, 1954c: 4-5). My estimates of egg brood range from 50,000 to 200,000. Such large worker broods invariably seem to decrease in size perhaps to 10,000 to 60,000 at the age of full grown larvae. My estimate for the maximum size of egg broods is based primarily on one cluster of workers and brood removed from a statary bivouac. This cluster measured about 30 by 50 mm. and included 270 minor

and intermediate workers, two major workers, and an estimated 55,000 eggs. The estimate was made by comparing the volume of 9,500 counted eggs with the volume of the remaining uncounted eggs. Although the number of eggs in the sample taken can be quite accurately estimated, the proportion of a total brood which this sample represents can only be based on impressions of the size of egg clusters found in bivouacs at the end of the statary phase or on the first nomadic day.

Empty cocoons have also been found during statary phases of *hamatum* colonies with worker broods, but these cocoons were the same size and thus easily confused with those from nondoryline ants that are booty.

Perhaps there is considerable cannibalism by the recently emerged callows about which Schneirla writes (1952: 255), "During the first few days after their emergence they are confined mainly to the bivouac, where they feed voraciously and are almost incessantly in motion." Callows were definitely seen feeding on booty; how much they may feed on the army ant brood is unknown. In all large samples of brood, it was possible to find a few larvae of the army ants which looked somewhat shrunken or shrivelled. These looked the same as larvae on which the ants had been seen feeding in laboratory nests. Such larvae were difficult to spot in masses of brood, because they apparently were seldom torn apart by the ants until they were greatly reduced in size. The ants bit at them and apparently put small punctures in the larvae, and then fed on oozing juices. Sometimes no fluid could be seen to come out of the larva, but a worker would bite and lick it repeatedly. Since such larvae were never abundant, I suspect that most cannibalism occurs in the egg or youngest larval stages.

In one colony of *hamatum*, '55 H-E, workers during the statary phase opened at least several thousand cocoons when the worker pupae were still completely white. A sample of these pupae was examined, and no abnormalities were found among them. A physogastric queen had been removed from this colony on the previous day, and the bivouac had been considerably disturbed along with part of its support in the search for the queen. Perhaps this disturbance had initiated the tearing open of these cocoons. Opened cocoons and the pupae were not noticed the day when the queen had been taken, and most if not all of them must have been dropped below the bivouac within twenty hours of the removal of the queen. It is not known whether the workers ate any of the brood. Presumably they fed to some extent in the process of tearing out the

soft pupae. Similar disturbances of two statary bivouacs of *hamatum*, without taking the queens, did not result in attacks on the cocoons.

Because of the difficulty in estimating accurately the size of a colony, it is even more difficult to determine whether the colonies change in size. Schneirla (1949b: 25) reported that the population of colony '46 H-B was still "considerably less" than would be expected after four broods completed development while the colony was being studied. This case is probably the best evidence for high mortality within the adult worker population. The most important factors limiting population size were considered to be "climatic hazards incurred in extra-bivouac activities" (Schneirla, 1949b: 76). Many workers are also killed by species attacked during raiding (Schneirla, 1956b: 384), but no estimates of the amount of mortality have been made.

Sexual Broods and Colony Division of *Eciton hamatum*

Reproductives are generally produced during the dry season when some colonies have broods consisting *at the time of emergence* of about six queens and 1,000 to 2,000 males. It is not known whether the size of a colony influences the laying of reproductive-producing eggs during the dry season. Some colonies have been found with sexual broods at the same time that larger colonies had worker broods. The "impact" of the dry season (or a sufficiently dry period in the rainy season) is considered to be the necessary factor causing the queen to produce a sexual brood (Schneirla and Brown, 1950: 350; 1952). How the "impact" of the dry season directly or indirectly affects the queen has not been suggested. The following observations suggest that additional factors may play an important part in the production of sexual broods: (1) all colonies of *hamatum* in the same locality do not have sexual broods at the same time or in the same dry season; and (2) other species of *Eciton s. str.* and other genera of army ants have sexual broods in the rainy season.

Colonies with sexual broods have nomadic and statary phases comparable to those of colonies with worker broods. However, there are many differences in behavior which have been reported primarily by Schneirla (1948, 1956a) and Schneirla and Brown (1952). Several of their most important findings will be summarized here.

Unfortunately there is only one record of a colony whose sexual brood was seen in the egg stage. The size of this brood was estimated at 15,000+ and as "quite as numerous as with a worker

brood at the corresponding time" (Schneirla and Brown, 1952: 10, 12). Only an estimated 2,000 adult males developed from this egg brood. General impressions gained from sampling other colonies also convinced Schneirla and Brown that sexual broods normally are greatly reduced, not only during the larval stage, but also in the pupal stage. The much smaller size of the sexual broods compared with worker broods undoubtedly is an important factor in the rapid development of these male and queen larvae, in part because there would be more food available per larva. The total development time for sexual broods is about 43 or 44 days compared with 45 to 47 days for the worker broods with the difference attributed to a shorter larval period for sexual broods (Schneirla and Brown, 1952: 17). However, the total volume or tissue bulk of the sexual broods may be considerably smaller than that of the worker broods (based on the estimated size of worker broods being more likely from 30,000 to 60,000, compared to 25,000 as estimated by Schneirla and Brown, 1952: 12).

There is no doubt that the broods of reproductive larvae stimulate the workers more than a brood of worker larvae in spite of their smaller numerical size. Evidence of this has been given by Schneirla (1948) and Schneirla and Brown (1952). One aspect of this stimulation is the more frequent formation of "roadways" of workers along emigration columns.

Partly because of increased excitation of the workers and the antagonism between queens during the last two or three days of the statary phase, a bivouac with a sexual brood is apt to shift more than a bivouac with a worker brood. The queens emerge before the males, and the virgin queens may start to move away from the old queen and each other. They may move out of the bivouac and stay in the center of a cluster of workers adjacent to the bivouac.

The complex and highly variable process of colony division takes place during and directly following the emergence of the males. At this time the colony also has a young brood of eggs and larvae and will start a nomadic phase. A colony may or may not divide when it has a sexual brood, and the old queen may be superseded, or she may remain with part of the colony. It is probably impossible for a colony of *hamatum* to divide into more than two colonies, and colonies which do divide may not divide into equal halves. In all cases it appears that the two daughter colonies emigrate in opposite directions (*i. e.*, the emigration routes form an angle close to 180° at the statary bivouac). A connecting column may remain between the two daughter colonies for a day, and if

one queen is removed during the first few days after division, undoubtedly the two daughter colonies will fuse into one. For additional details see the paper by Schneirla (1956a).

At the start of the nomadic phase, immediately after the emergence of the males, each male along the emigration route is in or followed by a group of workers. The workers are in these groups not only because the workers are attracted to the males and cling to them in the emigration column, but also because the males have more difficulty running along the route and their larger bodies cause some blocking of the emigration column. On subsequent emigrations the number of workers with each male decreases probably due in part to a decreasing attraction for the workers. In addition, the males become stronger or more active with the result that they can shake off the workers by fanning their wings and can run away from the groups of workers.

Although the males are attracted to lights at night, they do not leave the bivouacs during the daytime. Schneirla (pers. com.) found that the males of colony '48 H-27 flew out strongly when their bivouac was accidentally broken open during the daytime after the eighth nomadic day. Most flights start along the emigration routes or at the old and new bivouacs during the emigrations (Schneirla, 1948: 100-101). The males are slow fliers with little ability to maneuver and no ability to defend themselves against predators. Few males of *hamatum* were taken at several lights on Barro Colorado Island during 1952, 1955, and 1956, even when colonies with alate males were known to be present on the island. The dates and times when males were taken during 1956 are as follows (with the number of males in parentheses): 9 May, 8:00 p. m. (1); 10 May, 9:00 p. m. (1); 29 May, 12:30 a. m. (1); 29 May, 9:30 p. m. (2); 3 June, 8:00 p. m. (2); 4 June, 9:30 p. m. (2); 29 June, 8:30 p. m. (1); 4 July, 9:00 p. m. (1). These dates can be grouped into three pairs of consecutive nights and a final pair five days apart. Probably all the males came from three or four or at most six colonies.

The males probably are not capable of mating for about three days after their emergence. A flight may also be essential before the males can mate (Schneirla, 1948: 107-108). Therefore, males probably cannot mate with queens from their own colony during the first few days or a week after the queens have emerged. This allows time for fertilization by males from other colonies, if there are any with sexual broods nearby. However, if no other males are in the vicinity, the probability increases that after they have

flown, males from the same colony will mate with the queens. Schneirla (pers. com.) captured a young queen from colony '48 H-12 at a time probably not more than four or five days after she emerged. This callow queen had already been fertilized, as a later histological examination by Dr. Roy Whelden showed. Following the flight from the parent colony, the males soon lose their wings. The genitalia also may become somewhat more protruded, but they have never been seen as widely spread as in males of *Labidus* and some other army ants. Within two weeks of their emergence, almost all males have left their parent colony. Their scarcity in other colonies and the short periods when the males were taken at lights are evidence that the males die within one to three weeks after emergence. The fact that I have never seen a male army ant of any species with frayed wings further supports the hypothesis that the males are short-lived and weak fliers.

Activity Cycle of *Eciton hamatum*

The activity cycle of alternating nomadic and statary phases was first described by Schneirla (1933), and all his papers on army ants since that date contain some information related to this cycle. A diagram of the cycle is given in figure 1. With a worker brood, the nomadic phase is typically 17 days, but may range from 16 to 18 days regardless of rainy or dry seasons. The statary phase ranges from 17 to 22 days. However, the mean for this phase during the rainy season is 19.6 days, and the mean in the dry season is 20.3 days (Schneirla 1957a: 107). Because of the confusion of dry and rainy season records published by Schneirla (1949b) and Schneirla and Brown (1950), these means should be computed again. With a sexual brood, the length of the nomadic phase is considerably shortened to eight to 13 days, but the statary phase remains about the same length (Schneirla and Brown, 1950: 322-323).

The initial emigration beginning a nomadic phase has been attributed primarily to the stimulation of the older workers by the newly emerged callow workers (Schneirla, 1938, 1957). These callow workers emerge almost exclusively on the last statary day and first nomadic day. It is rare to see a cocoon being carried on an emigration on the first nomadic day, and none could be found when this entire emigration of colony E-121 was watched. The new brood of eggs and young larvae are considered to be of negligible importance for exciting the workers at this time. The callows have been considered "hyperactive and voracious" (Schneirla, 1944c: 181),

but samples from two colonies which I have watched did not show these characteristics. (This does not imply that they do not or could not arouse the workers adequately for an emigration.) For the most part the callows stay together in large groups in the bivouac. They do not take part in the raids of the first statary day and are found in considerable numbers in raids only when they are approaching the color of the older workers about five days after emergence (Schneirla, 1938).

Schneirla (1938, 1957) holds theoretically that as the stimulation of the workers by the callows decreases, the stimulation by the larvae increases, maintaining the large daily raids and nightly emigrations. The brood of eggs and young larvae is in relatively tight clusters covered with minor workers. As the larvae increase in size, they become more active and more widely distributed throughout the bivouac, and additional workers come in contact with them.

The daily raids during the nomadic phase are clearly larger on the average than those during the statary phase. Schneirla has further reported that larger raids occur and the emigrations are longer near the end of the nomadic phase compared with the beginning (1944c: 182). No supporting quantitative evidence has been presented to demonstrate these differences. When raids and emigrations were observed, it appeared to me that the size of the raids, but not necessarily their maximum distances from the bivouac or the distances between bivouacs, increased during the nomadic phase. Moreover, the emigration distances for one colony, '46 H-B, did not show such an increase when they were graphed (see figure 7). This graph shows a slight decrease in the emigration distances at the end of the nomadic cycle for this colony, which was studied for a longer period than any other colony by *hamatum*. The mean distances for these emigrations, grouped by pairs starting with nomadic days one and two, and not counting the 17th nomadic day in the second cycle, are: 130, 133, 183, 162, 179, 143, 132, and 161 meters. Using the method of moving averages (mean distances for days one to three, two to four, etc.), one can compute the following means: 138, 150, 144, 155, 176, 172, 159, 173, 179, 163, 154, 123, 146, 137, and 146. Both methods indicate slightly longer emigrations in the center of the phase. Moreover, the short emigrations of 120, 30, 110, and 15 meters occurred respectively on the 10th, 12th, and twice on the 14th nomadic days which are all before there is appreciable spinning by the larvae.

As Schneirla and Brown (1954) have reported, colonies at the

end of the nomadic phase more frequently form bivouacs in enclosed or more sheltered sites. Common bivouac sites are inside hollow logs or holes in the ground. During the last nomadic day and first statary day, larvae are carried out of the nest for spinning. As the larvae spin cocoons, the resulting drop in stimulation of the workers initiates the statary phase.

During the statary period raids are much smaller and less frequent, and on some days there may not be a raid. The bivouac stays approximately in the same place, but there always is some shifting of its exact position. The bottom of a statary bivouac of colony '46 H-A inside a hollow tree varied up and down through a height of 18 cm. from day to day (Schneirla, 1949b: 40). Part of this shifting may not indicate any movement of the center of the cluster, but rather an addition or subtraction of ants around the periphery as the ants leave or return from raiding. On other occasions the entire bivouac has been seen to shift one to three meters deeper into a hollow log. I have seen an actual shift in progress on only one occasion. In this case the ants had an "emigration" column between the two bivouacs about a meter apart, and the queen must have run along this column. In other cases it is possible that the bivouac may have shifted by the addition and subtraction of ants from opposite sides of the bivouac over a period of several days, rather than by having a complete movement of the entire colony along a column. Some shifting of the bivouac may be important to give relief to those ants making up the major supporting walls of the bivouac. In three cases a colony of *hamatum* moved more than five meters during the statary phase, but these moves followed considerable destruction of the original bivouacs and their supports.

At the end of the nomadic phase, the queen may show slight traces of physogastry, but during the first week of the statary phase her gaster apparently reaches its maximal size (Schneirla, 1957a: 118). Presumably the eggs are laid primarily during a week in the middle of the statary phase (of 18 to 22 days). Unfortunately, there appears to be no reliable data to indicate the beginning and end of the egg laying period. Eggs have been laid in laboratory nests at a rate of 178 per hour for a seven hour period (Schneirla, 1944c: 167). At this rate the queen could lay about 43,000 eggs in ten days. This total approximates those of other brood estimates.

Throughout Schneirla's many papers it is repeatedly emphasized that the brood is primarily responsible for the activity cycle because of the brood's stimulation of the workers. Before the work of

Schneirla, it was thought that the ants exhausted the supply of food in the area of the nest and then were compelled to move to find additional food. Abundant evidence against this simple but conventional and traditionally strong hypothesis has been given repeatedly by Schneirla. Nevertheless, as Schneirla (1957a: 121-122) has also pointed out, emigrations are a necessary adaptation, since army ant colonies are too large to be able to find adequate supplies of food within the restricted areas around their nests for a long period of time. One aspect of this problem which has not been adequately studied is the quantity of booty which is brought in to the nest and how this may affect the distance and duration of the raids and the length of the emigration. Emigrations vary in length from a few meters to several hundred meters usually for no apparent cause. The influence of the abundance of food on the direction and distance of raids and emigrations can be seen most clearly when the ants find an especially rich source of booty, such as a large wasp nest, and increase their raiding to that source. They may subsequently form a large booty cache and a bivouac at that spot. However, when the ants appear less successful, it is more difficult to determine whether the distances of the raids and emigrations are affected. In addition, the behavior of the larvae may be directly related to the abundance of food within the bivouac. No data are available to indicate whether larvae which are well fed are quieter and thus stimulate the adults less than hungry larvae. Such a relationship might be predicted on the basis of other species of insects.

Interrelations Among Individuals of *Eciton hamatum*

Adult workers rarely exchange food or secretions by their mouthparts, but they frequently clean or lick each other's bodies. An individual worker also licks its own body with its maxillae and labium. Although no quantitative measurements were made, it appeared that most of this cleaning was concentrated on the tip of the abdomen and the front legs.

There was no indication that any of the workers were attracted more to majors or cleaned majors more than they cleaned smaller workers. However, adding a major to a dish of workers caused more excitement than adding a submajor or smaller worker. This was not true if a small worker was taken from a dish with a queen and added to a dish of workers without a queen. Workers which had been with the queen apparently carried some queen odor which greatly excited the other ants. Brown (1960) has reported some evidence that a chemical, possibly from the mandibular gland, is

released from the heads of majors. This chemical alarms and attracts other workers which will attack the head of a major when it is severed from the ant's body. These majors may be adapted for alarming the rest of the colony, but all workers seem to have this same ability, if to a lesser extent. The majors alone possess large, shiny heads with elongate, hook-like mandibles, and there are no intermediate shapes between these and the more triangular mandibles of the submajors. The majors readily would sting and bite prey, but they were never seen to carry any booty or brood.

No major or submajor was ever seen being carried by another worker. Moreover, there appeared to be an inverse relationship between the size of the workers and the extent that they were carried. The youngest callows were also carried much more than older callows and dark workers, and more workers were carried at the ends of emigrations than at any other time during raids or emigrations. In numerous cases these pairs of workers have been aspirated from columns. As soon as they were aspirated into a vial, both workers would run around actively, and there was never any sign that one of them was injured. The only time the two could be distinguished was when one was different in color or size from the other. No callow worker was ever seen carrying any other worker. Perhaps only slow, quiet workers are picked up by the more active individuals. In this way workers that are lagging behind at the old bivouac are picked up and carried along by other workers. The smallest workers which are carried most frequently are also the slowest moving and the last to emerge from cocoons.

The workers seemed to be more attracted to callow workers than to other older workers. Not enough observations, however, were made to reach any strong conclusions. The mature workers assist the callows to emerge by tearing the cocoons. Callows also emerged from cocoons isolated from workers, but considerably fewer emerged in a given time and more died in their cocoons. After the callows have emerged, they show a distinct tendency to stay together. When bivouacs containing callows are broken open during the first or second nomadic day, the callows to a large extent are concentrated in large masses. After several days they become completely integrated throughout the colony. Schneirla (1944a: 3) has also reported that there is a gradual appearance of the callows in the raid columns during the first five days of the nomadic phase. In the laboratory young callows usually die before older workers. Among the older workers the smallest individuals generally die first, and the majors are the last to survive. Under more adverse

conditions the same relationship holds, as shown by Schneirla, Brown, and Brown (1954: 283) for workers tested in a metal pan at a relative humidity below 60%.

As shown in the discussion of sexual broods, the workers are considerably attracted to the callow males, the attraction decreasing over a period of several days judging from the number of workers on each male. Queens which are callow may or may not be more attractive than old queens, judging from the results of colony divisions where old queens are sometimes superseded. Presumably the relative attraction of the various queens at the time of a colony division determines which queens survive in the daughter colonies (Schneirla, 1956a: 54-55).

Army ant queens invariably die when separated from their colonies. All queens which had been kept in the laboratory with a few hundred workers or less died within ten days, and about half of them died within four days (Schneirla, 1944c: 171). A queen kept "with her colony for more than two weeks in the laboratory" died within four days after she was segregated with a small group of workers. Queens with their colonies can live in the field at least four and one-half years (Schneirla, 1956b: 402).

When a queen was found in a bivouac, she typically was surrounded by a tight mass of workers which remained around the queen in a laboratory nest, making it impossible to observe her. When only about ten workers were placed in a dish with a queen, the queen normally was much more active than she was with the larger mass of workers. Workers followed her as she ran about the dish, and they frequently rode on her abdomen or thorax. After one or two days fewer workers stayed on or close to the queen. The workers licked the gaster of a queen more frequently than any other part of her body and never were seen to feed a queen or touch her mouthparts with their own. Moreover, no queen was ever seen to feed independently in laboratory nests, although on a few occasions she appeared to drink a little when crushed booty or cotton soaked in water was held against her mouthparts with forceps. Schneirla also reported that the workers were more attracted to a physogastric queen than to a contracted queen (1944c: 169). When the queen is laying, small drops of "fecal material" are deposited between the spurts of eggs. These are "evidently much relished" by the workers (*l. c.*). I have never been able to determine the source of these drops when watching physogastric queens of *hamatum* or other species. Perhaps the drops are not fecal material.

Workers sometimes spent more than an hour resting on the gaster of the queen in laboratory nests. These workers frequently licked the abdominal terga, and records were kept of the number of times workers licked or kept their mouthparts over the individual terga. With the queen and workers running and turning frequently, it was difficult to tell how often the workers were actually licking the queen. Therefore, the counts are based on the positions of the heads of the workers. Workers were recorded only if they remained in a given position for at least two seconds. The same ant was not recorded more than once, unless it had moved away from the queen or shifted its position to a different segment. The queen was moving intermittently so that the workers frequently shifted position or were brushed off. Ants with their heads over the junction between two terga were recorded with the more anterior tergum. By this method an ant in a position for two seconds was recorded with equal value to one there two minutes. In spite of their limitations, these data do show a differential attraction in the case of a contracted queen (E-123). The frequencies were measured over a period of two hours and were recorded as the number of ants per segment (see table 4).

Several conclusions seem to be warranted as a result of the above observations. The workers showed no indication of an attraction to the anal region of the contracted queen (even when she remained stationary for several minutes). They rested most frequently with their mouthparts over the first and second gaster segments and especially at the junction between the first and second segments. This position undoubtedly results in part from the fact

TABLE 4.—Relative Attraction of Workers to Parts of Queens.

SPECIES	Queen number	Ali-trunk	Petiole	Segments of gaster				
				1st	2nd	3rd	4th	5th
Eciton hamatum	E-123	×	×	27	16	11	1	0
E. dulcius crassinode	E-143	×	6	18	12	4	7	4
Eciton mexicanum	E-170	6	3	0	3	4	2	1
Nomamyrmex esenbecki	E-164	1	5	8	21	25	29	28

× = no record made but little attraction to this part of queen; for further explanation see text.

that a worker can more easily ride on the larger and more level anterior segments of the gaster of the queen than on the more sloping posterior segments. The workers seldom rode on the queen facing posteriorly. When they did ride in this position, they usually were standing on the thorax or petiole with their mouthparts over the first or second gaster segments. In addition, the workers on the floor of the dish kept their mouthparts (or heads) close to the first and second terga most of the time. Probably the chemical which is responsible for the attraction to the queen is secreted from glands at this part of the gaster. However, these data are considerably different from similar records for two other queens as can be seen in table 4.

Hagan (1954b: 14-16) reported that two pairs of glandular cell masses were segmentally arranged "in the vicinity of the vulva" of a *hamatum* queen. Each mass consisted of approximately 50 cells, each of which has one ductule extending through the exoskeleton. The opening of the ductule is enlarged and apparently surrounded by small setae. Hagan wrote, "It is quite possible more of these glands are present in other segments, but only the two pairs were observed." His investigation was primarily concerned with the reproductive system, and no information was given on the body wall or glands of the anterior part of the gaster.

Schneirla (1944c: 163) has reported, "Workers are especially attracted to pieces of cardboard formerly in use as floors for the queen's cell, and will collect in the one of two compartments in which a queen has rested for a time." This reaction may be due to a queen odor, but no adequately controlled experiments have been reported.

Workers will stand on top of a pile of larvae for more than a half hour without moving or licking them. At other times the squirming movements of the larvae seem to attract workers which are standing on or near them or running over them. These workers may then shift the larvae or may lick them. Since the larvae are extremely inefficient at crawling across even rough surfaces, it is essential that the adults bring food to them or take them to food. The workers apparently feed the newly-hatched larvae while licking them. However, the older larvae seldom if ever are fed directly from the mouths of workers. The adult ants pile booty on top of the larvae and larvae on top of booty. The larvae are frequently found inside sclerotized pieces of booty, such as head capsules or legs where the adult ants would not be able to feed.

It has been suggested on the basis of the reduction of the proventriculus (Eisner, 1957: 478, 485; Eisner and Brown, 1958) that the adult dorylines may eat solid matter. However, their method of feeding indicates that only liquid food is usually ingested. The mandibles were seen to be used when an ant was pulling or tearing food, but they were never used like those of a grasshopper for chewing food. The reduction of the proventriculus is more apt to be connected with the weak development of trophallaxis.

An adult carries a larva by holding it usually near the anterior end and only occasionally near the posterior end. The worker's mandibles usually grasp the first or second thoracic segments of the larva. Because the anterior end of a larvae is narrower than the posterior end, workers may find the anterior end easier to grasp. However, these workers can easily carry larvae with a larger diameter, and it appears that the workers are attracted to the anterior end probably by chemical rather than morphological factors.

When the larvae are fully grown, the adult workers carry them out of the bivouac to areas of fine loose detritus, such as powdered rotton wood. There the larvae spin their cocoons in the loose surface layer. When the cocoons are nearly or completely finished, the workers grasp the cocoons near the narrower posterior end and carry them back into the bivouac. In laboratory nests the cocoons are ignored more than larvae, but the workers will often pile them in one place and stand on top of them. Schneirla (1944c: 177) reported "they are presumably neutral in importance or may actually exert a quieting effect upon the workers that clutch them in their mandibles, somewhat as the pressure of thumb-in-mouth pacifies an infant." When the callows are ready to emerge, their movements appear to attract workers which then help the callows to get out of the cocoons.

Eciton lucanoides Emery

Eciton lucanoides Emery has been divided into two subspecies, *lucanoides s. str.* and *conquistador* Weber, by Borgmeier (1955: 262-269). However, since the males of both subspecies and the queen of one are unknown, there is a strong possibility that these are two distinct species. A total of 24 specimens from only four samples of the former subspecies from Peru, western Brazil, and Bolivia were examined by Borgmeier. The latter subspecies is known from about ten colonies found in Costa Rica and Panama (including Barro Colorado Island). Although these few records indicate the species is generally rare, Schneirla and Brown found

two colonies, compared with three of *hamatum* and one of *burchelli*, "during a five-day survey of the forested Candelaria area above the confluence of the Pequeni and Boqueron rivers" [Panama] (Schneirla, reported by Weber, 1949: 5). On Barro Colorado Island all collectors have apparently found only one *lucanoides* colony out of over 500 colonies of *Eciton*.

Biological observations have been made only on the subspecies *conquistador*. The two colonies found by Schneirla and Brown had column raids which were quite strong between 11:00 and 11:30 a. m. However, *lucanoides* is considered to have raid columns that are "characteristically narrower than those of *hamatum* and both in width and in the behavior of workers on them are roughly transitional between *hamatum* and *rogeri*" [= *mexicanum*] (Schneirla, reported by Weber, 1949: 6). *E. lucanoides* is similar to *hamatum* but somewhat darker in color. The two species would be easy to confuse in the field. Consequently, whenever weak columns of *hamatum*-like army ants are found, especially at night, one should examine the ants carefully to see if they are *lucanoides*. Their food also appears to be the same as that of *hamatum* (*l. c.*).

Only one emigration of *lucanoides* has been described (Nevermann, reported by Reichensperger, 1934: 241). Larvae were carried during the middle period of this emigration, and the queen was taken in a cluster of workers after all the brood had passed. Following the queen, some staphylinids were seen about 11:00 p. m., and at 11:30 p. m. the column ended. Thus, as would be expected of a primarily subterranean species, this emigration was later than the average *hamatum* emigration. Schneirla and Brown (1950: 313) reported one colony emigrated about 140 meters, but they did not watch this emigration.

Bivouacs have been found in three hollow trees, one hollow log and in the dense crown of a fallen tree (Schneirla, reported by Weber, 1949; Borgmeier, 1955: 265; and Nevermann in Reichensperger, 1934: 241). These records indicate that the bivouacs were in well-sheltered but nonsubterranean locations. The three nests for which dates are given were all found between 27 October and 15 November during the height of the rainy season. The species has distinct broods and probably has an activity cycle similar to that for *hamatum*. No sexual brood has been found.

The meager data above from raids, bivouacs and one emigration suggest that this species is approximately as epigaeic as *E. vagans* and less epigaeic than *hamatum* and *burchelli*.

Eciton burchelli (Westwood)

E. burchelli and *hamatum* apparently have identical ranges, except the latter species has not been found on Trinidad. Although Borgmeier (1955: 183-192) did not separate *hamatum* into subspecies, he divided *burchelli* into the following subspecies: *burchelli s. str.* (from Brazil and Paraguay), *foreli* Mayr (Honduras, Costa Rica, Panama, Colombia, and Ecuador) *parvispinum* Forel (Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama), *urichi* Forel (Trinidad) and *cupiens* Santschi (Colombia, Venezuela, British Guiana, French Guiana, Brazil, Peru, and Bolivia). Among these localities given by Borgmeier, there are several cases in which two subspecies are sympatric over considerable areas. Additional collecting will have to be done before an accurate description can be made of the variation within the species. Specimens from Barro Colorado Island and parts of Panama south and east of the Canal Zone are *burchelli foreli*. Specimens from Chiriqui are *b. parvispinum* (Borgmeier, 1955: 189).

Raids of *Eciton burchelli*

The organization of raids by *E. burchelli* and their relation to emigrations have been studied intensively by Schneirla (1940, 1944). *E. burchelli* feeds on a greater variety of food than any other species of *Eciton* observed on Barro Colorado Island. Even though the amount and kind of prey which *burchelli* captures is influenced largely by its manner of raiding in swarms, the behavior of the individual workers is also of great importance. The workers seem more easily excited, quicker to attack and more pugnacious, and they have a stronger bite and a more potent sting (to a person) than any other species of *Eciton*. Their method of raiding by large swarms (discussed more fully below) results in their driving numerous animals out from under leaves or other objects. A column raid is much less effective in flushing out animals, primarily because the ants cover a much more limited area in any one vicinity during a short space of time. Any animals flushed out by a column raid would be able to escape the ants by moving a relatively short distance away. Animals must run or fly a greater distance to escape the onrush of the ants in an advancing swarm front two to 15 meters wide.

When one first watches a swarm raid of *burchelli* progressing across the forest floor, it appears that the ants kill all kinds of arthropods. Unfortunately, a thorough survey of the food of any species of army ant has never been made even from a qualitative

standpoint. Careful observation, however, revealed that along the ground, as in the trees, *burchelli* killed more ants than any other group of arthropods. Wasps, Orthoptera (*s. lat.*) and spiders were probably next in abundance among the booty. However, a large proportion of the potential prey of the forest floor always seemed to escape. Even when the ants attacked nests of social insects, although the brood was completely killed, most of the adults escaped. Some arthropods were never attacked, and casual observations indicated that 30% to 50% of the arthropods attacked escaped being killed. Most of these arthropods avoided capture by running away in front of the swarm, flying, or climbing up vegetation. Others ran or jumped to a spot in the middle of the anastomosing columns behind the swarm front. If they landed between columns, the ants sometimes did not find them. However, if they landed on a column or in the midst of the swarm, they almost invariably were killed in a few seconds. As Schneirla (1945: 176) has pointed out, even *burchelli* colonies do not come close to depleting the supply of prey around a statary bivouac, and any area cleared of prey may be rapidly repopulated.

The raiding workers attacked almost anything that moved, including a blade of grass, a vertebrate, or an arthropod. The movement of the object was of prime importance since the ants attacked a blade of grass only when it vibrated, and they immediately ceased attacking it after one or two bites. Many times an arthropod was seen to escape being killed when it remained motionless. The same species, on other occasions when it moved, was promptly killed. The importance of the movement of the prey can be demonstrated by vibrating or shaking a tettigoniid or cicada in the area of the swarm. Before the vibration, the insect may have been ignored, but with the vibration the ants quickly attacked the insect and continued to attack it as long as the vibration persisted. The motion of the arthropod was undoubtedly not the only factor here. The ants varied greatly in the speed, intensity or efficiency of their raiding and were usually much less efficient than at the height of a maximal raid. Probably the number of workers around any potential booty object also was important in that 100 workers appeared more than twice as efficient in attacking as 50 workers possibly due to mutual stimulation among the workers.

If an arthropod struggles considerably after it is attacked, it appears to be torn up more than if it remains quiet. Probably for this reason, most larvae and pupae are intact when carried back to the bivouac. The intermediate workers do almost all the attacking,

dissecting of prey, and carrying of prey. The majors assist in the attacks especially when the prey is large or struggles considerably, but no major worker was ever seen carrying any booty. When a piece of booty was too large to be carried by a single intermediate worker, as many as seven workers were seen carrying it. Small workers frequently and large workers occasionally ride on the booty or on the ants carrying it. (See figures 8 and 9 of workers carrying booty.)

There are no records of *burchelli* eating any plant material, not even vegetable oils and nut meats, which are eaten by some other dorylines. Vertebrates will be attacked if they persist in staying in the swarm of raiding ants. I have seen mammals like the tapir (*Tapirella bairdii*), anteater (*Tamandua tetradactyla*), and coati (*Nasua narica*) being driven out of areas where they were feeding by swarm raids of *burchelli*. The tapir has a tough skin, but it is vulnerable to bites or stings between its toes. The coati and tamandua eat other ants, but not the army ants.

Once a small dead snake was found at 9:30 a.m. in a mass of *burchelli* about three meters from the bivouac. Probably the ants

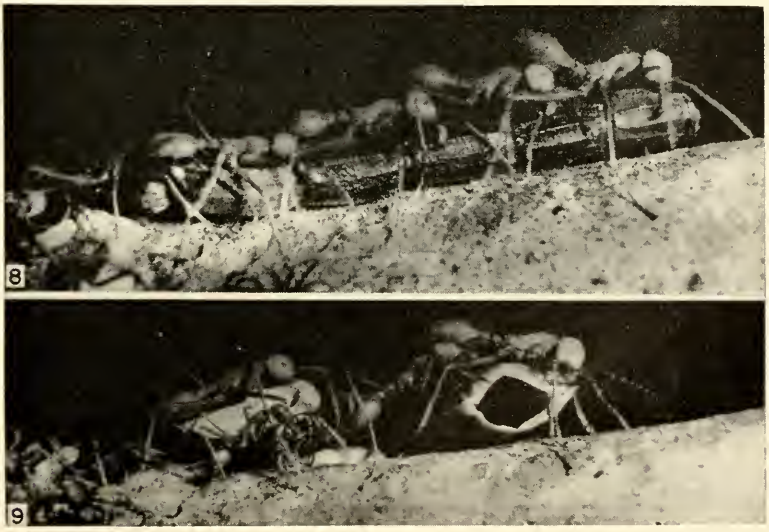


Figure 8.—Tail of a scorpion being carried by three submajors and an intermediate worker of *E. burchelli* in raid column. A fifth worker at left end is partially riding on the tail but not helping to carry it.

Figure 9.—Submajor of *E. burchelli* on right is carrying tergum and sternum of an orthopteran (cockroach?) while another worker is partially riding on the booty. Large worker behind it is carrying white wasp pupa.

had killed it a few hours earlier at the start of the raid. During the two hours after the snake was first seen, hundreds of workers bit and pulled on the snake and managed to tear it partially open. During those two hours the ants had clearly been successful at eating a small part of this snake. On the following morning the completely stripped but intact skeleton (38 cm. long) was found in the same spot, but it is not known how much of the snake was eaten by the *burchelli* and how much was eaten by other ants or insects. Although this is the only time that I have seen a vertebrate which was probably killed by army ants, iridescent blue lizard tails about six centimeters long were seen occasionally in the raid columns. Presumably the lizards usually escaped; at least no other parts of them were seen being carried back to the bivouacs. No other pieces of vertebrates were ever seen being carried in ant columns, nor were they found in refuse deposits.

Since *burchelli* raids up into the tops of the tallest trees, one would suspect that they may frequently kill nestling birds. Schneirla (1956b: 389) states, "I have seen snakes, lizards, and nestling birds killed on various occasions; undoubtedly a larger vertebrate which, because of injury or for some other reason, could not run off, would be killed by stinging or by asphyxiation. But lacking a cutting or shearing edge on their mandibles, unlike their African relatives, the 'driver ants,' these tropical American swarmers cannot tear down their occasional vertebrate victims."

The mandibles of ecitonine workers, other than the *Eciton* majors, work like pliers which clamp on the prey. The mandibles do not cross or overlap more than a slight amount at their tips, and they have a poor toothed cutting edge. The mandibles appear to function more like wire cutters with edges which abut. All the booty is primarily pulled apart with little actual cutting, although a worker may gnaw at one spot for more than 15 minutes. The mandibles of *Dorylus* (*Anomma*) are long and curved with much sharper toothed cutting edges which overlap and apparently cut like scissors. *Eciton burchelli* and all other Neotropical army ants cannot strip flesh from vertebrates or are much less efficient than *Dorylus* (*Anomma*) at such action primarily because of these differences in the mandibles.

Both *hamatum* and *burchelli* attack the nests of many species of Polybiinae and Polistinae (Vespidae). However, *burchelli* kills a greater proportion of the adults; and since it goes higher into the trees, it must prey on some species that are above the level of *hamatum* raids. Likewise, *burchelli* more frequently raids ant

colonies in trees, especially *Camponotus sericeiventris* (Guerin), the largest carpenter ant on Barro Colorado Island. The largest ponerine found there, *Paraponera clavata* (Fabricius), is also frequently attacked by *burchelli*, which is successful at killing the workers in subterranean nests even though these ants are about twice as long as the largest majors of the army ant. When various species of ants were raided by *burchelli*, it appeared that they often made almost no attempt to resist the army ants. Other ants, such as species of *Atta* and *Cryptocerus*, either were not attacked, or they resisted strongly and were rarely killed even though they are smaller than the *Eciton*.

When either *burchelli* or *hamatum* attacked a colony of wasps or nondoryline ants, many of the adults of the attacked species, and especially the returning foragers, were seen around the periphery of the nest or resting on near-by vegetation. One would expect that the swarm raid of *burchelli* would be more successful than the column raid of *hamatum* at capturing some of these insects displaced from their nests.

Pieces of Orthoptera are among the most frequent prey which can be identified in raid columns. Blattidae, Gryllidae, and Tettigoniidae are the most common families killed. Hemiptera may or may not be killed, possibly dependent in part upon their abdominal scent glands. Coleoptera are frequently attacked, but often the ants are incapable of killing the larger and more heavily sclerotized species. Beetles such as Scarabaeidae, Carabidae, and Elateridae normally retract their legs and remain motionless. The ants frequently pull off all the tarsal segments and then abandon the beetle.

Schneirla (1956b: 389) reported that walking sticks [Phasmidae] are not killed because of "repellent chemicals, as tests show, as well as through tonic immobility." Four phasmids were promptly killed when I attempted to repeat this experiment in the laboratory. All the specimens were too badly fragmented to be determined, but at least two species of wingless phasmids were killed.

Odonata are rarely killed, as one would predict. Nevertheless, around the statary bivouac of colony '55 B-IV, I picked up 120 wings of dragonflies (Anisoptera). Evidently at least 30 dragonflies had attempted to rest under the log where the ants were clustered and had been caught when they touched the bivouac. In a similar manner, *burchelli* may kill a fair number of insects such as Diptera and Hymenoptera which one would not expect the army ants to be able to capture.

Ticks were reported by Schneirla (1956b: 389) to be immune from attacks. All the ticks which I have observed with *burchelli* were Ixodidae, and none of the ants attacked any of the ticks. It did not make any difference whether the ticks were gravid or ungravid, nymphs or larvae; the ants ran up to the ticks and then turned away. Perhaps the coxal glands of the ticks secrete a substance repellent to the ants. However, in laboratory nests *burchelli* was seen to walk on two ticks and no repelling of the ants was observed.

Numerous species of spiders and especially Lycosidae, which are common on the forest floor, were killed by *burchelli*. No tarantulas were seen killed, nor were their remains found in refuse deposits; however, Schneirla (*l. c.*) reported that they are killed. On several occasions, tarantulas were seen to lift their legs in succession and shake *burchelli* workers off of them. Other spiders occasionally escaped by hanging down from plants by silk threads when raiding ants drove them off the plants. Scorpions were frequently killed, but the whipless whip-scorpions, Tarantulidae, always darted out of the path of the ants and even were observed to eat *burchelli* workers.

Termites also seem to be largely immune from attack (Beebe, 1917: 521; Schneirla, 1956b: 389), but a few termites were found among booty. Perhaps only occasional foraging termites are captured since the army ants were not seen to attack numerous termite nests in the areas of the ant raids.

On the basis of the fragmentary but numerous observations given above, it is evident that *Eciton burchelli* is selective in its feeding. A thorough study would undoubtedly reveal many other arthropods which are not attacked or not eaten by these ants. *E. hamatum* and other species of army ants appear to be even more selective than *burchelli*.

Swarm raids of *burchelli* in the nomadic phase start near dawn when *hamatum* raids begin. However, their inherent differences are immediately apparent. Workers swarm out in all directions from the bivouac of *burchelli* and quite thoroughly cover the ground. The raiding workers within fifteen minutes have started to narrow down the swarm to one or two primary directions. Usually within the next hour the swarm is further directionalized and has the form shown in figure 6, except that it is smaller. Maximal raids reach their peak about 11:00 a. m. when they are approximately the size shown in figure 6. The swarm front may shift to

one side or another in "flanking movements" as it progresses across the forest floor, but in spite of these shifts it usually maintains a fairly constant direction. If a particularly rich source of food is found at one edge of the swarm, a smaller subswarm may advance in that direction. At other times, the main swarm may shift toward the source of booty. If the swarm comes to a tree, it may or may not go up the trunk. Perhaps chemical trails of other colonies or species of army ants or other insects attract the swarm up these trees. A raid swarm will go more than 20 meters up the largest trees even though little booty will usually be found in the region of the main trunk.

A continuous column of workers running in both directions connects the raid swarm with the bivouac at all times. The base column is usually three to 12 ants wide, or about twice the width of the base columns of *hamatum* raids. As with *hamatum*, there is a siesta period of decreased activity followed by an afternoon resurgence leading up to an emigration if the colony is in the nomadic phase. During the siesta period or at any time when the raid is greatly diminished, the swarm pattern becomes much less obvious. At these times the swarm of ants may cover only about a square meter of the ground, and in some places the ants appear to be column raiders. The swarm makes little progress, and a high percentage of the ants may be moving in the direction of the bivouac. The various factors connected with the broods which influence the size of *hamatum* raids, also affect the raids of *burchelli*. Raids of *burchelli* at their maximum development never extend as far from the bivouac as the raids of *hamatum*. Judging from the decrease in the size of a bivouac after a raid is in progress, both species of *Eciton* have approximately the same proportion of the colony taking part in a maximal raid. Since the colonies of *burchelli* are at least twice the size of those of *hamatum*, the number of ants on the raids must be correspondingly greater. Unlike *hamatum* which usually has raid columns extending in two or three directions when it has a large raid, *burchelli* usually has a single raiding system in one direction.

It has been reported by Schneirla (1949b: 74) that *burchelli* is less apt to raid during the statary phase in the dry season than in the rainy season. The decrease of 14% in the number of days with raids was based on one colony which had a sexual brood, and that brood might have been more responsible for the decrease than the dry season itself. A more valid comparison would be based on the

number of colonies raiding on the individual days of the statary period. Some decrease in raiding may occur during the statary phase in the dry season, but no adequate quantitative data are available.

The swarm raids of *burchelli* differ markedly from column raids of other species of army ants in the large number of birds and flies that accompany the ants. There are about ten species of antbirds which commonly follow the swarm raids of *E. burchelli* on Barro Colorado Island. A brief study of the behavior of these birds around the swarm raids has been made by Johnson (1954). The two species of antbird which are present over most swarms are the Bicolored Antbird, *Gymnopithys leucaspis,* and the Spotted Antbird, *Hylophylax naeviodes.* These appear soon after the raid starts and follow the swarm front as it advances. The calls of both of these species are a repeated low "cherr" or "churr." These calls are useful indicators of the location of swarm raids of either *E. burchelli* or *L. praedator.* (Bates [1863 v. 2: 357] also reported antbirds over *E. drepanophorum,* but there are no subsequent reports on the type of raids of this army ant.) Dr. Alexander Wetmore, who has studied birds for many years in Panama, has told me that he has repeatedly and only found swarm raids of army ants by tracing the calls of the antbirds.

These antbirds primarily feed on insects escaping from the ant raids rather than on the army ants (Johnson, 1954: 44; Schneirla, 1956b: 390). However, there is evidence that some of the birds accompanying the swarms do feed to a considerable extent on the army ants. Ihering (1912: 235) reported that the stomach of one specimen of *Neomorphus geoffroyi* which had been accompanying a swarm raid of *E. burchelli* was filled with the army ants. There is some additional evidence that some of the antbirds may feed on the army ants (Bequaert, 1922; Wheeler, 1932: 307). Nevertheless, most of these birds do not eat the army ants, or if they do eat them, it is primarily because the ants are attached to other food. The stomach of a *Hylophylax naeviodes,* which was accompanying an army ant swarm, contained "spider parts but no ant remains" (Howell, 1957: 93). The stomach of a *Formicarius analis* also contained no ants, but a lizard was found in it. Howell (1957: 92) commented, "As one of the Barecrowned Antbirds had also eaten an *Anolis*, it may be that small lizards form a regular part of the diet of these formicariids." Since it is known that some of the antbirds eat the army ants as well as spiders, lizards, and Orthoptera, a more reliable conclusion on the extent that these birds feed on

the army ants will have to await a more thorough study of the stomach contents of large series of birds.

The calls of the antbirds mingle with the buzzing of numerous flies and the rustling of dried leaves as spiders, amphipods, cockroaches and other arthropods flee from the advancing ants. During the dry season the flies accompanying the swarm, the fleeing arthropods, and the thousands of ants running on the dried leaves produce a distinctive sound. This is less evident in the rainy season when the forest floor is thoroughly soaked. On one occasion I was first attracted to a swarm raid of *burchelli* by the sound of hundreds of waterbugs fleeing up the bank from a stream bed. The stream was almost dry, and the bugs had been resting mainly on the ground when the raiding ants drove them up the bank.

A large swarm raid of *burchelli* will be accompanied by over a thousand flies which hover over the ants or dart from leaf to leaf in the center of the swarm or just in advance of the swarm. These flies have been thought to be parasitic on the ants, but most if not all of them are parasitic on insects flushed out by the ants. They have been discussed more fully by Rettenmeyer (1961b). These flies, like the antbirds, are not found over the column raids of other species of army ants. The flies can be heard for a distance of five to ten meters, and on several occasions I have found swarms by locating the source of this buzzing. Dr. Charles H. Curran, who, as a dipterist, was undoubtedly more conscious of the buzzing of flies than the calling of the antbirds, reported (1934a: 1), "In every case in which I located armies of ants I was attracted by the noise of the flies."

Emigrations of *Eciton burchelli*

The increase in raiding activity that occurs after the siesta period when colonies are in the nomadic phase seems to take place at the same time with *burchelli* and *hamatum*. However, the emigrations of *burchelli* frequently do not start until after 6:00 p. m. which is somewhat later than those of *hamatum*. Some emigrations do not start until after 8:00 or even 10:00 p. m. Even when the emigrations start between 3:00 and 6:00 p. m., the queen does not usually emigrate until after 8:00 p. m. The times when queens were seen along emigrations are given in table 3. The somewhat later appearance of the *burchelli* queens compared with those of *hamatum* is attributed to a combination of the later beginnings of emigrations and the larger sizes of the colonies. It may also be true that the *burchelli* queens emigrate more frequently after about 50% of the

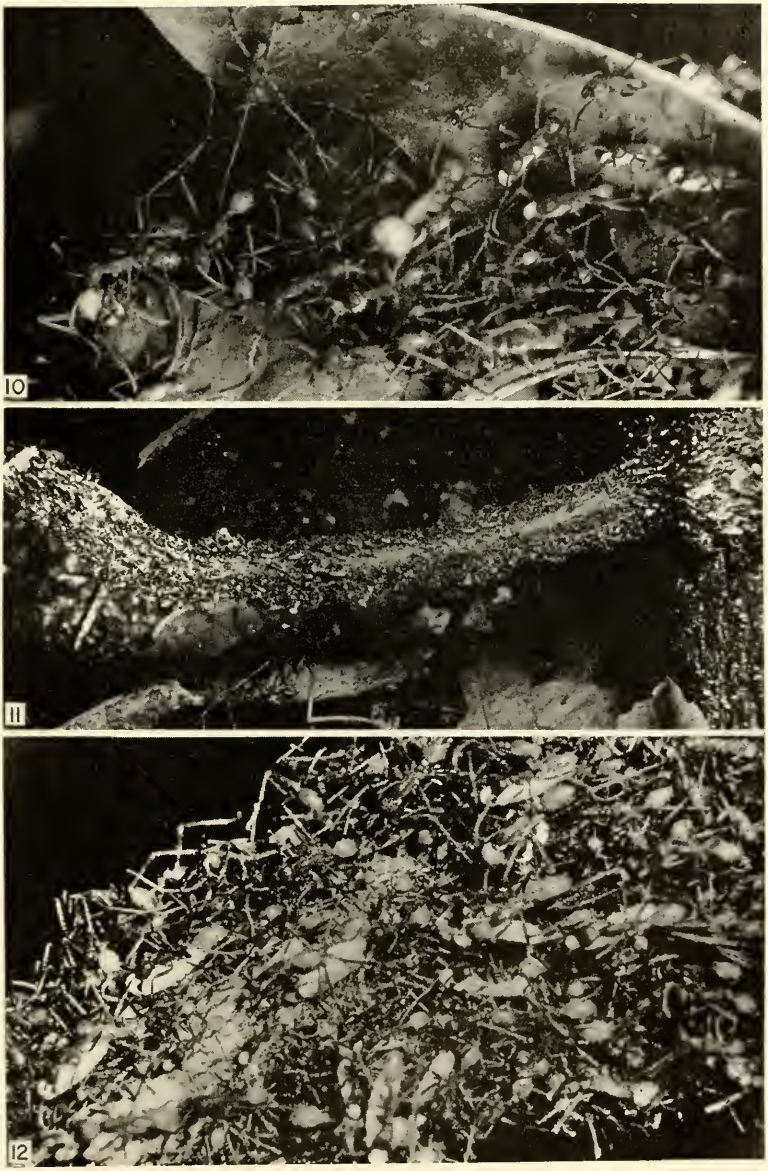
FIGURES 10-12

FIGURE 10.—Emigration column of *E. burchelli* showing ants holding edges of leaves closer together with their legs. Bodies of ants form a bridge over which other workers are emigrating. Ants on right are carrying worker larvae and booty.

FIGURE 11.—Emigration column of *E. burchelli* across liana about ten millimeters in diameter. Ants have made flanges on each side of liana which have tripled width of "roadway" over which other ants can emigrate. These flanges extend along column for about one meter where the liana forms a bridge from a log (at right edge of picture) to a small tree (out of the picture on the left).

FIGURE 12.—Close-up of emigration column with flanges in figure 11. Some ants are carrying worker-producing larvae which are held at one end by the mandibles of the workers. Army ants always carry objects under their bodies.

FIGURES 10-12



workers have left the old bivouac rather than nearer 90%. The earliest that a queen of *burchelli* was seen on an emigration was 7:45 p. m. This case may have been abnormal because I returned the queen to the bivouac at 10:15 a. m. the same day. Since the colonies are much larger than those of *hamatum,* emigrations which start near 7:00 p. m. may not be completed until about 3:00 a. m. the next morning. If there is a heavy rain during the night, an emigration may be prolonged into the daylight hours the next morning.

The emigration columns average about twice the width of those of *hamatum.* Since the swarm raids do not advance more than 75 to 150 meters from the bivouac, as a rule, the mean emigration distance is less for *burchelli.* The greater amount of traffic and the more easily excitable nature of the workers are probably the primary factors contributing to the greater development of ant roadways along *burchelli* emigrations (see figures 10 to 12). Colonies with broods of young larvae have weaker roadways than those with larvae almost ready to spin, and colonies with sexual broods have even larger roadways. The workers seem more highly excited by the larger larvae, and the difficulty in carrying the sexual larvae apparently further increases the ant roadway. Guard workers likewise are more common with *burchelli* and are increased with any disturbance or excitement of the workers.

The retinue of the queen on the emigration may consist of several hundred workers and is always larger than with *hamatum.* This greater mass of workers appears to slow the progress of the queen, and when she moves slowly more workers join the retinue. On the few occasions where a queen was seen emigrating along a smooth log several meters in length, the number of workers accompanying her greatly decreased compared to those with her when she was crossing leaves. If there is considerable disturbance of the column, the number of guard workers will increase until there is a solid row of them along both sides. These solid rows of guards were never seen with any other species of *Eciton.* Light seems to disturb an emigration of *burchelli* more than one of *hamatum.* The greater disturbance may be due more to the greater number of ants along the column rather than to a greater sensitivity of the workers to light. Otherwise the observations mentioned earlier regarding the queen and guard workers along emigrations of *hamatum* apply also to those of *burchelli.*

The same sequence of events also takes place during the emigra-

tions of *burchelli;* however, all stages are more prolonged due to the larger sizes of colonies. I rarely saw the end of an emigration because the last ants usually left the old bivouac after midnight.

Bivouacs of *Eciton burchelli*

Bivouacs of *E. burchelli* are similar to those of *hamatum* and are frequently found in the same sites such as the interbuttress spaces of large trees (figures 13 and 14). However, the bivouacs of *burchelli* in addition to their larger size are distinctly "more epigaeic" or more elevated than those of *hamatum.* Schneirla, Brown, and Brown (1954: 279) have shown that *burchelli* has fewer subterranean and many more elevated bivouacs than *hamatum.* Bivouacs of *burchelli* did not touch the ground in 33% of 270 cases, whereas those of *hamatum* were elevated in only 7 per cent of 440 cases. Moreover, when bivouacs of *burchelli* were elevated, they were usually more than one meter from the ground, whereas those of *hamatum* were below one meter. A colony of *burchelli* will apparently bivouac in a sheltered spot at any height in a tree. Using binoculars, I have watched emigrations and raid columns which went up trees to bivouacs at least 20 meters above the ground.

The bivouacs of *burchelli* shift by small amounts during the statary period even when they are well enclosed and not disturbed. Although statary bivouacs were not observed every day, three colonies are known to have shifted their bivouacs from five to more than 55 cm. at least several times throughout that phase. Possibly these shifts were primarily due to the subtraction and addition of workers resulting from raiding, but at least some shifting occurred in the absence of a raid. Shifting may be influenced by the presence of a sexual brood which is usually in the section of the bivouac away from the old queen. This bipolarity may normally result in some lengthening of the bivouac.

Refuse deposits of *Eciton burchelli*

Eciton burchelli is the only species of army ant included in this report which has extensive epigaeic refuse deposits. As a direct consequence of its feeding on a variety of adult arthropods, there is a considerable amount of refuse from the more sclerotized parts of the prey. This refuse, empty cocoons and dead workers are put by the ants in more or less distinct areas which I have termed refuse deposits. Short columns extending out from the bivouac are here called "refuse columns" whether or not they go to distinct refuse deposits. Many ants seen along these columns were not

FIGURE 13.—Bivouac (dark mass) of *Eciton burchelli,* colony E-253, between buttresses of large tree on 17 August 1956. Colony is in nomadic phase with worker larvae almost mature. Width of bivouac is about 45 cm.

FIGURE 14.—Lower edge of bivouac of *E. burchelli,* colony '55 B-1, photographed on 5 February 1955 as ants were moving from this statary site in a large tree. White objects scattered among workers are empty cocoons which dropped to refuse deposit on ground when ants left.

carrying any refuse but appeared to be just wandering back and forth from the bivouac. The workers defecate along the columns as well as in the refuse deposits, and the fecal material may form a distinct white trail during the statary phase.

Because workers of *burchelli* emerge over a period of at least six days, their empty cocoons can be found in the refuse deposits from one day before the last statary day to the fourth nomadic day. Empty cocoons are most abundant on the first nomadic day, and on the second nomadic day they are much more abundant than with *hamatum* colonies on that day. The number of cocoons on the second nomadic day may give the area around the bivouac the appearance of a statary site, except that much less booty refuse is found, and the site would usually be less enclosed or sheltered.

Size of Colonies and Broods of *Eciton burchelli*

Schneirla gives fewer estimates of the sizes of colonies of *burchelli* than for *hamatum;* but these estimates, like those of *hamatum* colonies, have been increased in his later papers. An early estimate for a "very large" colony was "more than 200,000" (Schneirla, 1949b: 37), and his largest estimate is 300,000 to 1,500,000 workers (Schneirla, 1957b). I estimate 150,000 to 300,000 workers are in the smallest colonies after a colony division.

Three and one-half quarts of preserved workers and worker-producing larvae taken on the 14th nomadic day from colony '55 B-IV-N were completely counted and found to contain about 77,800 workers (including 1,600 majors) and 104,800 larvae. This sample was taken about 11:30 a. m. when many workers were on a backtracking column resulting from removing the queen from the emigration column on the preceding night. Probably less than one half of the workers were taken. On this basis the colony consisted of 180,000 to 250,000 workers. This colony was at the end of the first nomadic phase after a colony division, and it was one of the smallest if not the smallest colony of *burchelli* which I have ever seen. Many *hamatum* colonies are of equivalent size. Probably about 90% of the larval brood was taken, indicating a total brood of 116,000 for this daughter colony. The brood total probably is accurate to within 20,000 larvae.

The second daughter colony, '55 B-IV-S, was considered to be about twice as large as '55 B-IV-N. A sample of four quarts of preserved workers and larvae were taken from this colony, but this was clearly less than one half of that daughter colony. This sample

must include about 100,000 workers and 150,000 larvae. On the basis of the relative sizes of the two daughter colonies, '55 B-IV-S probably had approximately 500,000 workers. The parent colony would thus have had about 700,000 workers and a brood of 250,000 to possibly 350,000 full-grown larvae. This astonishing brood was laid by the single queen of the parent colony. Estimates of brood size published by Schneirla are lower than these but have been increased from "25,000 or more" (1949b: 37), to "60,000 or more" (1956a: 2), to "120,000 +" (1957b: 266). Schneirla (pers. com.) estimated the size of a brood of young worker larvae at somewhat more than 220,000 based on a count completed in 1956 of two randomized eighths of a brood sample from colony '46 B-I (of which more than 90% was estimated to have been collected on 8 to 9 June 1946).

Estimates based on samples from other colonies are comparable but less accurate than the ones given above for the '55 B-IV colonies since smaller proportions of the colonies were taken. Samples of 100 ml. of tightly packed ants of approximately the normal size distribution and not including brood, range from about 4,000 to 6,000 workers. These figures are essentially the same as for *hamatum*. However, each of these samples was less than 1/100 of a large *burchelli* colony.

Estimates based on emigration rates are somewhat lower than the above and start at 300,000 workers for colonies of medium size. Unfortunately, the maximum rate of emigration in ants per second could not be determined accurately. Maximum emigration times are not known, but some colonies must have over 500,000 workers based on estimated emigration rates and durations of over eight hours.

The total egg production for a *burchelli* queen would be between 55,616 and 66,100 eggs if based on counts of ovarioles and oöcytes determined by Hagan (1954a, 1954c). Although the estimate of the number of ovarioles might be inaccurate, one would expect that the discrepancy between Hagan's estimate for an entire brood and my counts of larvae lies primarily in the oöcyte count. Possibly the eggs develop at such a fast rate that the first eggs have been laid before the last eggs to be laid can be distinguished in the ovarioles.

Since a large percentage of an egg brood of *burchelli* has never been counted, there is no evidence that a reduction in the size of a worker brood during the nomadic phase occurs, but perhaps the workers normally eat part of the eggs or larvae of a worker brood.

Sexual Broods and Colony Division of *Eciton burchelli*

Colonies of *E. burchelli*, like those of *hamatum*, may have a brood consisting solely of males and queens during the dry season. Observations on these broods and several subsequent colony divisions have been published by Schneirla (1948, 1956a) and Schneirla and Brown (1952). It was considered "quite possible" that colonies of *burchelli* have sexual broods earlier than *hamatum* (Schneirla, 1948: 91). Subsequent observations did not show as clear a separation of almost a month in the timing of these broods (Schneirla and Brown, 1952: 10). However, a tendency for *burchelli* to have males earlier is still indicated and is further supported by observations made during 1956.

Eleven adult males were taken between 17 March and 11 May 1956, compared with 11 for *hamatum* taken between 9 May and 4 July 1956. The males were taken on the following dates, and unless other data are given the males were all alates taken at lights in the laboratory clearing: 17 March (1 dealate from emigration column of colony E-132), 17 April (1), 19 April (1), 19 April (1 flew to light between 12:30 and 2:00 a. m.), 19 April (3 seen in the bivouac and 1 taken from emigration column of colony E-149, 1 dealate from emigration column of colony E-148), 28 April (1 dealate from emigration column of colony E-152), 10 May (1 taken at 8:30 p. m.), 11 May (3 taken at 8:30 p. m.).

Although worker broods often appear to be 100 to 300% larger in colonies of *burchelli* than in those of *hamatum*, the numbers of queens produced by both species are nearly the same; and the number of males (based on data from Schneirla and Brown, 1952: 10) is 50 to 100% larger in *burchelli*.

The oldest known *burchelli* queen was recovered after four years and two months, and she probably lived at least five years. Dr. Schneirla marked this queen, and I returned her to her colony, '52 B-IX, on 10 March 1952 on the second nomadic day when her gaster measured 11.9 mm. in length. When the same queen was found on 12 May 1956 in colony E-148 also on the second nomadic day, her gaster measured 14.0 to 14.5 mm. The later measurement was made at 3:45 a. m. shortly after the first nomadic emigration had been completed. In order to determine whether complete contraction of the gaster had occurred, the queen was again brought to the laboratory on the sixth nomadic day. At this time the gaster was the same length, and thus two to three millimeters longer than measurements of other queens in the middle of the nomadic phase

made by Schneirla (1957a: 119). These measurements suggest that as the queens get older their gasters contract less during the nomadic phase so that they may appear continually physogastric. Before the work by Schneirla it was generally assumed that contracted queens were young and physogastric queens mature or old. Schneirla (1944c; 1958: 218-219) has shown that the age of the queen is not the primary factor in the changes observed in the size of the gaster. The record for the queen of colony '52 B-IX indicates that "physogastric" queens should be observed to determine whether they are actually laying eggs.

A dealate male was taken on 17 March 1956 from an emigration column of colony E-132 at 8:11 p. m. more than 30 meters from the old bivouac. No other males were found in the emigration column of E-132 which was watched continuously from 8:00 to 9:25 p. m. However, on the previous night between 6:30 and 6:40 p. m. one male (or possibly two) was seen five meters above the ground on the trunk of the tree in which the statary bivouac was located. The male was seemingly trying to join the raid column on which ants were returning to the bivouac located more than 12 meters up the tree. Twice the male flew away from the column but returned to it about a half meter away. Workers could be seen congregating around the male, but its ultimate fate could not be determined because of the height. This male did not come from colony E-132 which had a brood of callow workers. If colony E-132 had a sexual brood in the preceding nomadic phase, the adult males would have emerged about 12 February. The earliest record for alates of *burchelli* on Barro Colorado Island appears to be 28 February 1946 (Schneirla, 1948: 93). In addition, males probably never remain in the colony in which they are produced at the end of the statary phase following their emergence (*l. c.*).

On the same first nomadic emigration on which the dealate male was taken, the queen was taken at 9:25 p. m. Her gaster was clearly somewhat swollen and when the queen was etherized on the following morning her gaster was still 11.9 to 12.0 mm. long. This is near the average for queens on the second nomadic day (Schneirla, 1957a: 119). This queen must have laid the current and previous worker broods. Unless she developed with a sexual brood at an atypical time of year, she probably was at least one year old when taken from the emigration column. She did not have a greatly swollen gaster which might be expected if she were more than three years old if the case for the queen of colony '52 B-IX

is typical. Thus, the queen of colony E-132 was not a virgin and was probably between one and three years old.

On the morning of 18 March after queen E-132 had recovered from ether and was walking around in a petri dish, the dealate male found in the emigration column was added to the dish. Copulation started within one minute and the pair remained together from 10:15 to 11:17 a. m. For the first 15 to 25 minutes the male constantly moved his antennae and front legs in large arcs. Only occasionally did it look as though he was stroking the queen with his antennae. The male held the queen by his middle and hind legs, never with his front legs. He also grasped her petiole behind the horns with his mandibles (figures 15 and 16). At no time did he hold onto the horns themselves. The queen walked around a little during the copulation but was never very active. At times the pair tended to fall over on one side, and after photographs had been taken at several angles, the male was pushed completely to one side to get a better view of the end of the queen's gaster. The external genitalia were widely spread and kept outside the queen's gaster (figure 17). The turning of the dish, the taking of more than a dozen electronic flash photographs, and the tipping of the male may have shortened the copulation time. After being coupled continuously for an hour and two minutes the pair separated. The male was unable to walk and was immediately preserved. The queen walked around in the dish but was not as active as other queens kept in the laboratory for an equal amount of time. She was returned to her colony and later was seen in an emigration.

Schneirla (1949b: 44-46) reported observing two matings of *E. hamatum*. His observations differ from mine in two important details: (1) one mating continued for about ten hours and the other for at least one hour and 30 minutes, and (2) each male held one petiolar horn tightly in his mandibles. The petioles of *Eciton* queens and the mandibles of the males differ markedly among the species. The behavior of the males suggests that contact between the mandibles and the queen's petiole may be important for mating and perhaps for preventing interspecies mating.

It is clear from two of the above observations of mating that an *Eciton* queen sometimes mates more than once and may mate annually.

Activity Cycle of *Eciton burchelli*

The major features of the activity cycle of *burchelli* are identical to those for *hamatum* as shown in figure 1. However, more varia-

15

16

17

FIGURE 15.—Lateral view of copulating male and queen of *Eciton burchelli*. (Colony E-132, 18 March 1956).

FIGURE 16.—Anteriolateral view. The male grasped the gaster of the queen with his middle and hind legs. His mandibles are behind the petiolar horns. The queen walked around the dish during and following mating.

FIGURE 17—Posterioventral view.

bility is shown by *burchelli* in the length of the nomadic phase and in other aspects of its behavior (Schneirla, 1949b). This phase can last from 11 to 17 days compared with 16 to 18 days for *hamatum* when colonies have larval worker broods. In contrast the statary phase shows slightly less variability, varying from 19 to 22 days, whereas it ranged from 17 to 22 days in *hamatum* (Schneirla, 1957a: 107; Schneirla and Brown, 1950: 282). In the dry season the nomadic phase may be slightly longer than in the rainy season, but too few entire nomadic phases have been followed to make this conclusive. When a colony has a sexual brood, the nomadic phase may be decreased to nine or ten days (Schneirla and Brown, 1950: 322).[1] The statary phase is the same length when a colony has a sexual brood. (Colony '48 B-XVII [Schneirla and Brown, 1950: 306-307] had a statary phase of 25 days, but this colony did not emigrate until "all or virtually all" the males had emerged, whereas other colonies had males still in cocoons on the first nomadic emigration. Frequent sampling and other disturbance of the colony, especially the removal of two queen cocoons, possibly affected the length of the statary phase and the failure of the colony to divide.)

The statary phase does not start until after the larvae have been spinning for several days. Although *hamatum* larvae spun cocoons almost exclusively on the first and second statary days, those of *burchelli* spun on the last three nomadic days and at least the first three statary days. The proportion of the brood which is enclosed on any of these days is not known.

Although the initiation of the nomadic phase is attributed to the stimulation of the older workers by the callows, sometimes the first nomadic emigration occurs before one half of the callows has emerged. In *hamatum* colonies the entire brood or nearly the entire brood has emerged before the first nomadic emigration. Schneirla (1957a: 112) has attributed this difference in behavior in part to the differences in brood and colony sizes. Broods and colonies of *burchelli* are larger than those of *hamatum*, but from my observations I believe that the *proportion* of callows to old adults is much

1. Unfortunately, the lengths of the three nomadic phases observed by Schneirla for colony '46 B-1 were incorrectly given as 10, 10, and 8 days by Schneirla and Brown (1952: 17). They should have been given as 12, 13, and 10 days as one can determine from the data published by Schneirla (1949b: 30-32). The last figure in each group is for the length of the nomadic phase when the colony had a sexual brood. In addition, the first statary phase for this colony was given as 20 days rather than the correct 22 days. These corrections would also raise the total development times given in the table published in 1952 to 44, 44, and 41 days. These corrected total development times are still two to five days less than the total development times for *hamatum*. Perhaps a shorter total time of development does not always occur in *burchelli*, judging from two records of nomadic phases of 17 days reported by Schneirla (1957a: 107).

less for *burchelli* than for *hamatum* on the first nomadic emigration. My observations on the effect of light and vibration agree with those of Schneirla which suggest that *burchelli* workers are more readily stimulated than those of *hamatum*. A lower threshold for excitation of the workers combined with the larger colony size of *burchelli* may be largely responsible for causing this species to emigrate before a large proportion of the brood has emerged.

Callows of *burchelli* were not seen to take part in the raids of the first and second nomadic day. However, at least 50 callows were seen carrying unopened cocoons on the first nomadic emigration of colony E-110. This colony emigrated when about 40 percent of the callows had emerged and some major workers were still in cocoons.

Raids appear to get larger toward the end of the nomadic phase, but no quantitative evidence can be given to support this. Although no clear trend is evident in the lengths of emigrations throughout the activity cycle, there may be a tendency for colonies not to emigrate for one night near both the beginning and end of the nomadic phase.

Interrelations Among Individuals of *Eciton burchelli*

All the observations reported above in the section on interrelations among individuals of *E. hamatum* apply also to *burchelli*. An additional observation on the longevity of queens in the laboratory was made for *burchelli*. The queen of colony E-136 taken on 28 April 1956 at 9:10 p. m. was only weakly twitching on 1 May at 9:00 a. m. and therefore lived only two and one-half days in the laboratory.

The workers seem to be more attracted to the posterior margin of the first tergum of the queen than to any other segment. Perhaps glands for a "queen substance" are located here, but Hagan (1954b) did not report finding any hypodermal gland cells in the gaster of the queens of *burchelli*.

The workers were seen to carry larvae out of the bivouac to spinning clusters both during the day and night. At night there seemed to be slightly less traffic by the workers, but the size of the cluster and the number of larvae in it seemed to be the same. Colony E-156, when visited between 2:00 and 3:15 a. m. on the third statary day, had a column one to three ants wide and a second column three to five ants wide continually present between the bivouac and the spinning area. Less than ten percent of the ants in these columns carried larvae or cocoons. These columns and

the spinning areas were distinct from the refuse columns and deposits.

Eciton vagans (Olivier)

Borgmeier (1955) has divided *Eciton vagans* into seven subspecies on the basis of differences found among males and queens. However, he could not find subspecific differences among the workers. Almost all the observations on the behavior of *vagans* have been made on the subspecies *mutatum*, found on Barro Colorado Island, or *angustatum*, found in Mexico. The ranges of these two subspecies overlap in Costa Rica according to Borgmeier.

Throughout its range *E. vagans* appears to be much more rarely seen than *hamatum* and *burchelli*, although the number of colonies of each species may be approximately the same. A total of 13 colonies of this species was found on Barro Colorado Island during 1956, compared with 18 of *burchelli* and 32 of *hamatum*. The lower number of colonies of *vagans* probably can be more reliably attributed to the time and method of its raiding and emigrating rather than to a smaller number of colonies. These differences will be discussed below.

Although workers of *vagans* are slightly larger than those of *hamatum* and *burchelli*, they have a weaker bite. Moreover, when several dozen workers were running on my legs or uncovered hands, not one tried to sting.

Fragmentary evidence given below and that reported by Schneirla (1947: 5, 9) show that *vagans* has synchronous broods and probably has alternating nomadic and statary phases. There is no evidence to indicate how frequently this species may emigrate or how long the nomadic phase may be. The only evidence regarding the possible length of a statary phase is that based on the length of time that a worker brood kept in the laboratory remained in cocoons. This sample was taken from a bivouac of colony E-154 on 30 April 1956 when the brood was partially enclosed in newly spun cocoons. The previous day this colony was in the identical spot, but the brood seen consisted of unenclosed larvae. The first major worker emerged in the laboratory on 22 May which would indicate a statary phase of 24 days, if 29 April was the first day of that phase. Unfortunately it is not known how long the colony remained in the site where the sample had been taken. Moreover, samples of brood may develop at a slower rate or the adults may emerge later than those remaining with the colony in the forest

judging from a case when *hamatum* cocoons were kept in a laboratory nest. Since all broods of *vagans* which have been observed are synchronous, one would expect that *vagans* has statary and nomadic phases similar in length and regularity to those of *hamatum*.

Like all other ecitonine queens, those of *vagans* are short-lived in laboratory nests. The queen from colony E-212 was clearly dying at 9:00 a. m. on 12 July after almost three days in the laboratory. However, the workers with this queen also were either dead or dying. The death of the queen may have been hastened by a macrochelid mite which was feeding on a small amount of liquid along the posterior margin of the first gastral segment. The mouthparts of the mite were not inserted into the membrane between the terga, but this mite may have punctured the membrane earlier. No similar fluid nor macrochelid mite has been seen on any other ecitonine queen.

Raids of *Eciton vagans*

Eciton vagans feeds primarily on ants, judging from the booty seen in raid columns. Adult ponerines were among the booty, and more adult ants may be killed by *vagans* than by *hamatum*. Other adult insects are attacked, but no raid columns were seen to go up any vegetation more than a few centimeters above the ground. However, Fiebrig (1907a: 84) reported that *E. vagans* (det. Forel) raided a *Polistes* nest under the eaves of a house. He also reported that they attacked bees which possessed stings (*t. c.*, p. 87) [the exact insect was not named, but perhaps the honeybee or a wasp was the species attached]. A click beetle (Elateridae) which fell among some workers milling around a hole near a bivouac was immediately attacked. The number of ants attacking this beetle increased to about 50, and they bit, pulled and attempted to sting it for 40 minutes. The ants were then removed from the beetle and preserved. The beetle had lost four segments of one antenna, ten segments of the other, and all tarsal segments were injured or had been removed. Both hind tibiae were also partially pulled from their sockets. When the beetle attempted to walk, it could hold only one leg in a normal position; all the others stuck out at odd angles and were quite useless. As far as I could determine, the ants never were successful at stinging the beetle although they tried to sting repeatedly. The elaterid repeatedly clicked while it was being attacked and while I was examining it. Perhaps this clicking helped to increase the number of ants attacking the beetle.

If the beetle had not been collected, it probably would not have been killed but would have lost most of its appendages, since other species of army ants were seen to desert similarly maimed beetles.

The raids of *vagans* resemble those of *hamatum* except that the columns start from subterranean bivouacs and extend only 10 to more than 100 meters along the surface of the ground. In most cases it was impossible to tell whether the bivouac was near the hole into which the ants disappeared. Schneirla (1934: 317) reported that the "consolidation columns that connect the raiding front with the bivouac mainly follow a subterranean course, the advanced part of the raid forms on the surface a system of branches and anastomosing columns. . . . If little booty is taken, the ants withdraw along their principal trail into the ground, and may soon emerge at a point some meters removed to repeat the process there." These observations were made during the very dry month of June 1933 (Schneirla, pers. com.) and may be unusual for *vagans*. Although this extension of a subterranean system undoubtedly occurs to some extent when *vagans* raids, there was little direct evidence for it during my observations. Two colonies had raid columns which entered holes at two or more points along their extent. However, six or more colonies had raid columns extending along the surface of the ground for at least 25 meters and more than 100 meters in three cases. These started from bivouacs, and the ants did not shift to a subterranean route even though they were capturing no prey within 25 meters of the bivouac and were raiding during daylight.

No raid columns were seen between noon and 6:00 p. m., but some raiding must occur during that period since columns were seen at 11:50 a. m. About three fourths of the raiding observed occurred between 6:00 p. m. and midnight. Presumably raiding is frequent between midnight and 8:00 a. m., but observations were not as frequent during those hours. Only four colonies were found raiding between 9:00 a. m. and noon even though more time was spent searching in the forest during those hours than during any other period of three hours. Probably most raids start between 6:00 p. m. and 6:00 a. m.

On one occasion a small swarm raid of *vagans* was discovered at 10:50 a. m. The ants covered the ground as extensively as a swarm raid of *burchelli*. Accompanying the advancing swarm were several of the same species of Tachinidae which are found over swarms of *burchelli*. However, by 11:20 a. m. the swarm front had

narrowed to a strong, forked raid column. The bivouac was found only three meters from the spot where the swarm front was discovered at 10:50 a. m. A brood of almost full-grown reproductive larvae was found in the bivouac. A swarm raid clearly is not typical behavior for *vagans*, and this unusual swarm is probably attributable to increased excitement due to the sexual brood and the fact that the raid was observed close to the bivouac. Other observations indicate that raids of *vagans* usually do not start this late in the morning.

Emigrations of *Eciton vagans*

The times when emigrations of *vagans* start probably are more variable than those of *hamatum* and *burchelli*. Only three emigrations of *vagans* were observed during 1956, and these had started some time before they were discovered. The earliest one observed was an emigration of colony E-180 found on 31 May 1956 at 8:15 p. m. At this time much brood was being carried, at 8:50 p. m. the queen was taken, and at about 10:20 p. m. the last ants passed. The exact locations of either bivouac were unknown, but the observations were at least 15 meters from the old bivouac. This emigration may have begun on the previous night. However, on the night it was observed it probably started before 7:00 p. m. and may have started before 6:00 p. m. A backtracking column was seen along the emigration route about 24 hours after the queen was taken, but it is not known when this column was started.

When colony E-240 was discovered on 7 August 1956 at 8:15 p. m., it was emigrating with a brood of alate males. The column was immediately followed toward the new bivouac, but after about 50 meters the column became thin, and it was not followed further. Probably the emigration had started about 7:00 p. m. From 8:15 to 10:50 p. m. the emigration was watched intermittently, and the queen most likely emigrated during that period, although she was not seen. At 10:50 p. m. the column had decreased to a width of one or two workers, and no males were in it. Further details about this emigration are given below in the section on sexual broods.

A third emigration observed was that of colony E-219 discovered on 24 July 1956 at 2:30 a. m. This column followed the emigration route used 20 days earlier by colony E-204, *E. dulcius*, for several meters along the *edge* of a concrete sidewalk. However, in places on the surface of the sidewalk as well as across dirt and a lawn, colony E-219 deviated from the route of the *dulcius* colony. The

queen of colony E-219 was taken at 3:03 a. m., and the number of workers gradually decreased following the queen. Over 90% of the ants must have emigrated before the queen left the old bivouac, assuming her progress was not impeded. The end of the emigration column, like such a column of *hamatum*, had many ants running for distances of about 30 cm. toward the old bivouac and then turning and following the rest of the colony. One stray worker passed at 3:46 a. m., more than five meters behind the last ants. However, at 3:49 a. m. several backtracking workers came from the direction of the new bivouac. It is not known whether a steady backtracking column was started at that time, but this would appear to be exceptionally soon for a backtracking column. No observations were made during the day after the queen was taken, but on the following morning, 26 July, the backtracking column was still present but decreased between 7:00 and 8:00 a. m. It did not start again until about 4:00 p. m. About 7:00 p. m. an attempt was made to trap workers by placing a small laboratory nest with the colony's queen and a few workers in the center of the backtracking column. This nest was about 20 cm. square and 2.5 cm. high with a glass cover and two entrance tubes large enough for the major workers. Although the tubes were placed in the column for about an hour and *vagans* and other species of *Eciton* had previously run through the tubing, none of the workers entered the nest. When the glass cover was removed, no workers entered the nest chamber after an additional hour, and the queen was then placed in the backtracking column. She promptly moved toward the new bivouac. The promptness with which this queen and other *Eciton* queens moved toward the current bivouac suggests that either the trail is polarized or the ants have some other method for determining the direction toward the bivouac.

The retinue of workers accompanying the queen of colony E-180 was quite large and similar to an average retinue with a *hamatum* queen. There were some guard workers along the margins of the column, but these usually left their positions in a short time, and no continuous rows of guard workers were present at any time. The guard workers were always dark or old workers, even though numerous callows were in the emigration column, and about the same number of callows as dark workers were carrying larvae. No callow workers were seen being carried. This colony probably was in the middle of the nomadic phase judging from the size of the worker larvae.

The retinue with the queen E-219 had a small number of majors which were clearly more excited than majors which were running in other parts of the emigration. However, although the majors ran back and forth, spread their mandibles, and rapidly vibrated their antennae, they did not rear up with their front legs off the ground. Two intermediate workers were partly running and partly clinging to the gaster of the queen with their heads over her gaster. When the queen was removed, the retinue continued along the emigration without her with only a slight disturbance noticed. The retinue was not followed.

Since eggs were being carried, the emigration of colony E-219 was observed probably on or near the second nomadic day. Nevertheless, a few callow workers were carrying booty or army ant larvae, and only a few callows were being carried by dark workers.

The emigrations of *vagans* had no ant roadways except for the emigration with the alate males discussed below under sexual broods. Since *vagans* columns seldom left the ground and did not even travel on logs as much as *hamatum*, flanges of ants were not apt to be seen. Only a single small flange was seen when a colony had a worker brood. The emigration of colony E-180 travelled for about one meter across leaves of wild pineapple plants, and a small flange of workers was seen on one of the smooth leaves. This flange was continuously present for more than one hour before the queen was seen in the column.

Bivouacs and Refuse Deposits of *Eciton vagans*

On Barro Colorado Island only subterranean or well-sheltered bivouacs of *E. vagans* have been found; however, "more exposed bivouacs . . . were observed under other conditions in Southern Mexico (Schneirla, 1947)" (Schneirla, Brown and Brown, 1954: 279). In the paper published in 1947 (p. 5, 9), the two colonies of *vagans* discussed, colonies "J" and "X2," had bivouacs inside rotten logs or partially in debris under the logs. The majority of ants in both cases were apparently not in a large cavity but distributed throughout many small cracks and passages within the rotten wood. Neither of these cases should be considered as "exposed" in the sense of Schneirla, Brown and Brown (1954: 278-279).

Fiebrig reported that on at least several occasions *E. vagans* was found bivouacking in the subterranean nest of *Atta sexdens* or *Atta* sp., but it was thought that the army ants occupied only the more peripheral and less-used sections of the nests. The two ant species

were not seen together, and it was not known whether the army ants killed the leaf cutters (Fiebrig, 1907a: 86; 1907b: 154-155).

All the bivouacs of *vagans* which were located during 1956 were sheltered on all sides and were primarily underground. Although none was completely dug out, partial descriptions of these nests will be given since few nests have been reported. Colony E-154 was first traced to the bivouac on 29 April by following a thin raid column at 6:15 p. m. The ants disappeared under leaves, and when these were brushed away, the entrance to the bivouac was indicated by about a dozen phorids which were hovering over the hole in the ground. When the ground was vibrated by cutting a small liana, several hundred workers including many carrying larvae ran out of the hole. Dark workers and some rather dark callows pulled small leaves and pieces of leaves and dirt into the entrance hole almost blocking it completely. There was a noticeable air current on the slope of the hill, and this current or my weak headlight may have caused the workers to decrease the size of the hole. At 8:15 a. m. the following morning 5,000 to 10,000 workers were clustered on small roots running through a cavity 25 to 30 cm. in diameter. The origin of the cavity is unknown, but the absence of loose dirt in cracks around the cavity or on the surface of the ground suggests that it was not made by the army ants. The top of this cavity was almost 30 cm. below the surface of the ground. At a depth of 50 cm. at least four principal passageways continued downward to an unknown depth. A total of 2,375 workers plus 59 majors and 302 worker larvae and cocoons were taken. Probably these larvae had been brought to or near the surface of the ground for spinning while most of the brood and adults were considerably deeper in the ground. Many of the larvae taken were enclosed in thin, incomplete cocoons. No queen nor males were found. While I was digging up the colony, the odor of the ants increased considerably; but no flies other than the few phorids were seen near the hole.

Another bivouac was found on 9 July by tracing the small raid swarm and column of colony E-212 discussed earlier. A diagram of this bivouac as it would appear if viewed directly from above is given in figure 18. This is the only time a larval sexual brood has been found in a bivouac of this species. A large number of leaves and small branches covered the area of the bivouac, but these are not indicated in figure 18. The only large cluster of ants was hanging from a log about 15 cm. in diameter, from a small branch, and from the side of the large rock. This mass was com-

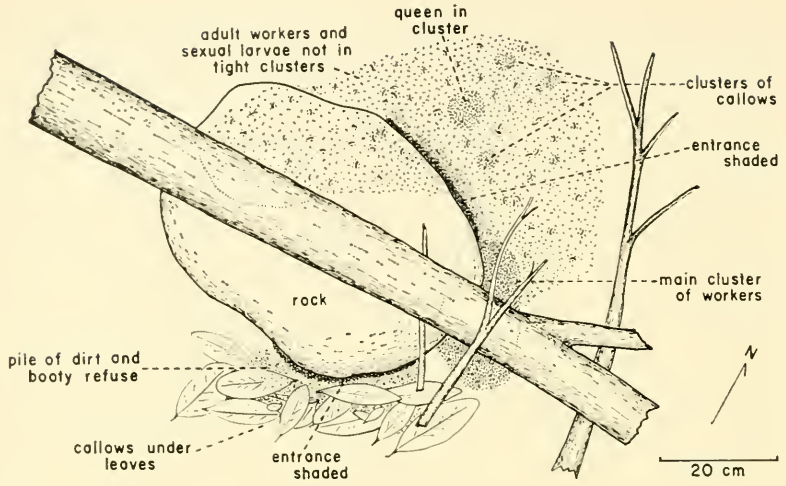


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FIGURE 18.—Diagram of bivouac of colony E-212, *Eciton vagans*, as it was found about 11:30 a. m., 9 July 1956. Numerous leaves and small twigs which covered entire area are not shown. Diagram indicates positions of workers hanging in one main cluster and dispersed under leaves on top of rock and around its north, east and south edges; sexual larvae scattered among workers, but absent in hanging cluster; callow workers primarily in two distinct clusters and scattered at south edge of bivouac; queen under leaves and twigs on surface of ground in small cluster of workers not including callows. Entrances on north and southeast edges of rock led to shallow cavities with scattered workers. (Cavities were possibly filled with workers before large number of raiding ants had left bivouac.) Refuse from booty was scattered mainly along southeast edge of rock with dirt excavated from under rock.

pletely covered by other small branches and leaves. No callows were among the ants comprising the outer layer of this cluster though there were some in the center. There were a few sexual larvae scattered throughout this cluster. Callow workers were primarily in distinct groups between leaves and on the ground under leaves. Some were along the south and southeast edges of the rock where there was a pile of loose dirt mixed with scattered refuse from booty. The booty refuse was so dispersed that it was impossible to get a sample of it without including considerable dirt. A few dark workers were seen carrying out dirt from under the rock and depositing it on this pile. No myrmecophiles were conspicuous near the refuse or nest before the bivouac was disturbed. Some ants were also going under the rock along the north side where a little digging apparently had been done by the army ants. A large proportion of the colony may have been underground.

The rock could not be moved, but attempts to push sticks underneath indicated that there was no large adjacent cavity.

Directly on top of the rock and throughout the stippled area north and east of the rock there was a layer of leaves and twigs. Under and among these were many workers which were fairly evenly distributed except for two distinct clusters consisting solely of callows and a third cluster of excited workers in which the queen was found. The clusters of callows had no older dark workers mixed with them, and these clusters did not rapidly disperse when disturbed like many of the darker adults, but remained together and appeared lethargic. In contrast, the cluster containing the queen had only a few callows but numerous dark workers including a noticeably greater number of majors than any of the other clusters. Many dark workers were running near the queen cluster, with some joining the cluster. Others left the cluster so that its size remained about the same. In addition, the majors were highly excited like those with queens of other species of *Eciton*. No tight mass of minor workers was found around the queen. It is possible that the queen moved a short distance as soon as I had disturbed the colony. However, it is quite certain that she was not on top of or under the rock. She may have been in the large hanging cluster or else on the ground nearer to the hanging cluster.

A brood of sexual larvae about three-fourths-grown was quite uniformly scattered on top of the rock and on the ground near the north and northeast sides. A few were in the hanging cluster. About two thirds of the larvae had no distinct groups of workers with them. Each larva of the remaining third was surrounded by a small cluster of up to 20 workers, some of which were clinging tightly to the larva. The larvae surrounded by clusters of workers were not concentrated in any one part of the bivouac. A total of 79 larvae was taken, which must have been at least half of those seen. Three or four larvae were partially shriveled at the time the bivouac was uncovered, indicating that the workers had been feeding on them. All the larvae taken are males; however, the small number of larvae and adults seen indicates that a large proportion of the bivouac, including probably a few queen-producing larvae, was underground. A small amount of booty was dispersed among the ants and not concentrated near the larvae.

Although a raid was in progress, it probably had started about 10:30 a. m., only about one hour before the bivouac was found. A small, steady amount of booty was being brought to the bivouac.

A large percentage of the colony could not have been participating in the raid at this time. These raiding ants probably came primarily from the hanging cluster and may have filled in shallow cavities under the north and northeast edges of the rock when the entire colony was at the bivouac. Approximately 10,000 workers plus 240 majors were taken from the bivouac. Over 50% of those seen must have escaped. Two samples of 100 ml. of ants included 2,258 and 2,837 workers (including majors). Since similar counts of *hamatum* and *burchelli* ranged from 3,000 to 6,000, these low counts reflect the larger size of the *vagans* workers and the higher proportion of majors. (An attempt was made to collect as many majors as possible, and the high proportion of majors, 1:40 intermediates, is not typical for this species.) Judging from the incomplete bivouacs and emigrations seen, colonies of *vagans* are probably smaller than those of *hamatum*.

Colony E-240 emigrated to a subterranean bivouac under a large palm with many stilt roots where digging was not practical. Workers were seen carrying dirt and wood detritus to small piles between the stilt roots, but the source of this material was not discovered. No booty refuse was seen in these piles. The night following this colony's emigration to this site, there was no emigration up until 8:05 p. m., and no observations were made after that time.

Sexual Broods of *Eciton vagans*

One colony of *Eciton vagans* was found with a sexual brood of larvae almost full-grown, and another colony was found with a brood of recently emerged alate males. The latter colony, E-240, was found emigrating on probably the second nomadic day following a colony division. A brood of eggs and young worker larvae was being carried, but only two eggs and two larvae were preserved. This emigration came out of a large brush heap and vine tangle in which the bivouac or at least the start of the epigaeic emigration column was located.

The workers were more excited than those seen on the two emigrations when sexual broods were not present. There were some places where a slight ant roadway, including bridges and flanges of workers, had been formed. However, these were not as well developed as those of *hamatum* colonies with comparable broods of alate males. Attempts to collect as many males as possible added to the excitement of the workers since a few ants would usually drop off when the males were picked up. My collecting caused

the formation of some small clusters of workers surrounding males along the emigrating route. These were similar to the clusters formed when a queen was stopped along an emigration. At least 50 of these clusters were formed, and some of them lasted more than 30 minutes. Almost every male in the column had at least one worker riding on him, or the worker was running along with its legs straddling the gaster of the male. At times as many as seven workers were seen on a male. A new genus of Histeridae, one thysanuran nymph (probably *Trichatelura manni* Caudell), and many small Limulodidae were seen riding on the males. Each male had a small group or retinue of up to 100 workers accompanying it. These workers were present partly because of the mechanical blocking of the emigration column rather than solely because of attraction to the males.

Along the emigration column it was impossible to tell whether the workers were only riding on the males and possibly licking them as they ran along, or whether the workers were actually clinging to the males by their mandibles. In the laboratory nests the workers continued to follow the males and were clearly seen to grasp the males with their mandibles. At times they bit the wings firmly enough to fold them. The workers also rode on the wings without grasping them with their mandibles.

The workers not only clung to the males but also licked the gasters and sometimes other parts of the males. A large amount of fecal material (?) from the males was deposited in the vials in which they had been brought to the laboratory. Some of the gasters became completely coated with this white fluid, and the amount of fecal material probably indicates that these males had recently emerged. The workers cleaned some of this material off the bodies of the males but also licked males which had no noticeable fecal material on them.

The fact that no males attempted to fly was an additional indication that the males had recently emerged. None of the males even attempted to spread his wings in the column whether or not workers were riding or clinging to him. After the workers had been removed from them and the males were dropped more than a meter, they still did not move their wings.

Although lights were watched at the laboratory for ten more days after these males were seen, no males of *vagans* were taken at the lights. Colony E-240 was located between 1,200 and 1,500 meters from the laboratory which may be farther than many of the males

would fly. The males in the emigration were much more affected by my light than the workers. Although these males invariably turned away from the beam of light, presumably they would become photopositive within a few days. Schneirla (1948: 106) reported that *Eciton* [apparently *hamatum* and *burchelli*] males withdrew from "very bright lights." My flashlight beam had a much lower intensity than the lights which attracted *Eciton* and other male army ants at the laboratory. The males must become photopositive, either several days following emergence or only after they have started flying. Most of the numerous males of *vagans* listed by Borgmeier (1955: 239-246) were probably taken at lights although this was not stated with any of the records.

The bivouac to which colony E-240 emigrated on 7 August was under a large palm tree where digging was not feasible. No ant clusters could be seen. On the opposite side of the tree from the emigration column a raid column extended and booty was being brought to this bivouac during the emigration. On the following night, 8 August, colony E-240 had raid columns at 7:05, 8:30 and 11:10 p. m., but there was no emigration. No males were seen among the ants milling around on the ground at the bivouac site, and there were no clusters of workers.

About 130 males were taken from colony E-240, and the total number of males was estimated at a minimum of between 300 and 500. The colony seemed to be small and may have been a daughter colony. If this number of males was half of the brood, the resulting estimate of a total brood of 600 to 1,000 is comparable to some counts of male broods of *hamatum*.

Since only 100 to 180 sexual brood larvae were seen in the bivouac of colony E-212, at least two thirds of the larvae were probably in a subterranean part of the bivouac which was not seen. Schneirla (1956a: 4-6) reported that colonies of *E. hamatum* are strongly bipolar with the old queen in one half of the bivouac and the sexual brood in the other half. In this regard it is interesting that the bivouac of colony E-212 did not show any clear separation of this type. Even if the queen had been in the hanging cluster before the bivouac was disturbed, in that cluster as well as throughout the area where the queen was found, there were scattered sexual larvae. Perhaps the queen larvae were in the subterranean part of the bivouac farthest from the adult queen. The cannibalism of several larvae that was occurring at the time the bivouac was discovered may indicate friction between the old queen or the workers associated with her and the brood.

Eciton dulcius Forel

Eciton dulcius dulcius Forel has been found only in Brazil and Argentina, and the other subspecies, *crassinode* Borgmeier, has been found only on Barro Colorado Island (Borgmeier, 1955: 203-209). The wide geographical area between these two subspecies suggests that they may be two distinct species rather than subspecies. All three castes of *dulcius s. str.* are known, but the male of *crassinode* has not yet been found or associated with the workers. In the forest *dulcius* is most easily confused with *vagans*, but the former lacks a spine on each posterior lateral angle of the head. No striking differences were noted between the behavior of these two species. Although the bites and stings seemed to be more severe than those of *hamatum*, the workers of *dulcius crassinode* did not bite nor sting as readily as either *hamatum* or *burchelli*.

Only eight colonies of *E. dulcius crassinode* were found on Barro Colorado Island, indicating that this species is the least common (or least commonly seen) of the five species of *Eciton* workers studied at that locality. *E. dulcius* has synchronous broods and has been seen emigrating with brood in the larval stage. A colony of *dulcius dulcius* which emigrated with cocoons containing males more than a week before their emergence probably was forced to emigrate since the subterranean bivouac of this colony had been dug up earlier the same day (Bruch, 1934b: 261-263). Numerous light callows were seen on two of four emigrations of different colonies in Panama, and one of these colonies had a brood of eggs and young larvae at the same time. Presumably the species has a nomadic-statary cycle, but the frequency of emigrations and the lengths of the phases are unknown.

Raids of *Eciton dulcius*

Judging from the booty being carried in columns, the most frequent prey of *Eciton dulcius* were Formicidae. Ponerinae were apparently captured more than any other subfamily of ants, and even *Paraponera clavata* (Fabricius) was killed. In Brazil Borgmeier (1955: 208) also saw *dulcius s. str.* carrying pupae of Myrmecinae and larvae and workers of *Dinoponera australis nigricolor* Borgmeier. Although *dulcius crassinode* was never seen to raid any wasps or other insects in trees, shrubs or on buildings, it would readily eat *Polistes* larvae and callow adults removed from capped cells and placed in laboratory nests. Bruch (1923: 173-174) reported that *dulcius s. str.* most frequently raided ants including the

leaf cutters, *Acromyrmex heyeri* and *A. silvestri,* and also raided *Polybia lechiquana.* On one occasion in Panama *dulcius* was seen to avoid a struggling partly crushed calliphorid fly dropped next to a raid column. This isolated case may be significant since flies seem to be avoided or only rarely attacked by other species of *Eciton.*

A sample of almost 3,000 workers taken from an emigration column on 2 April 1956 was given three large larvae and two pupae of *Polistes* on the following evening. These were readily attacked, and immediately there was a noticeable amount of trophallaxis between adult workers. For this transfer of large drops of fluid, the mandibles of both workers were not used but spread apart while the other mouthparts held the drops. The workers seemed to clean each other more after the food was supplied, and this cleaning may have been initiated by workers cleaning food off the mandibles of other workers.

Compared with the activity of any of the other four common species of *Eciton,* the epigaeic activity of *dulcius crassinode* appears to be more confined to hours of dusk or darkness. The only diurnal record from Panama is a raid column found at 5:00 p. m. However, Borgmeier watched a raid column of *dulcius s. str.* from 8:00 to 10:00 a. m. on 9 January 1934, but no locality or weather data was given (Borgmeier, 1955: 208). On Barro Colorado Island eight column raids of *d. crassinode* were found at night between 7:30 p. m. and 3:00 a. m. Since much more extensive searching for colonies was done during daylight, the scarcity of records for *dulcius crassinode* probably indicates that the species is even more nocturnal and subterranean than *vagans.* The interruption of an emigration at 5:40 a. m. and the presence of backtracking columns from about 5:00 p. m. to 6:00 a. m. are additional evidence that *dulcius* is active almost exclusively at night at least during the dry season and early rainy season. Although raids presumably always precede emigrations, there is no known way of predicting when the shift to an emigration may occur during a night. One colony, E-194, had raid columns continuously from 5:00 p. m. to after 10:45 p. m. when observations were ended.

On 24 February 1956 colony E-117 had a raid column which extended more than 100 meters and overlapped the area raided the previous day by *burchelli* colony E-111. The *dulcius* raid column probably followed the same trail as the emigration column of *burchelli* for short intermittent distances but clearly deviated from that trail in most places. The most striking result was that the raid

column of *dulcius* entered a hole in the ground directly at the bivouac site used by the *burchelli* colony on the previous day. It would appear to be disadvantageous for one species of army ant to follow such trails of other species especially since the strongest and most easily followed trails would be in the areas most recently raided. The odor of the refuse deposit along with the arthropods found in it may have attracted the *dulcius* colony to the site, but it is not known how near the bivouac of the *dulcius* colony was to the site of the *burchelli* bivouac.

Emigrations of *Eciton dulcius*

Only five emigrations of *dulcius crassinode* have been observed. Four of these most likely started in the evening about 7:30 p. m., and the fifth, which was found at 3:30 a. m., probably started after midnight. Perhaps it is significant that the latter case was a colony with a brood of worker larvae approximately half grown, whereas the colonies which emigrated earlier had broods of callow workers and in one case a brood of eggs and young larvae. The total distance of an emigration has not been determined, but one colony emigrated at least 91 meters and another emigrated over 100 meters above ground. In all cases where columns were followed, they led to a hole in the ground, and the exact position or extent of each bivouac was not determined.

The emigration of colony E-204 which was discovered at 3:30 a. m. provides evidence for interpreting the movements of all colonies of subterranean army ants. Although it is not known when this colony started its emigration, on 4 July 1956 the emigration column was at its maximum development at 3:30 a. m. and extended from dense low vegetation at the edge of the laboratory clearing to a hole about 20 meters away in the center of the clearing. No attempt was made to trace the column back through the dense second growth to the old bivouac. After 5:00 a. m. the amount of brood being carried gradually decreased, while the percent of smaller workers and the number of Phoridae increased, and by 5:40 a. m. the last ant had passed. After the last ant passed, four phorids ran along the emigration route. At 7:45 a. m. the same day there were no workers of *dulcius* at the hole into which the ants had disappeared earlier, and no columns were seen in that area of the clearing. The bivouac was partially dug out and a sample of almost 3,000 ants taken. About 5:00 p. m. a column gradually extended back along the previous emigration trail, and between

7:00 and 7:15 p. m. a strong column had developed continuing the previous emigration. Ants were carrying additional larvae to the same bivouac which had been partially dug out in the morning. This emigration column was only one to three ants wide or about half the width of the column in the morning. The number of ants emigrating fluctuated frequently during both observation periods, and at times the column stopped completely. In a few cases these fluctuations were partially due to my collecting, but at other times the interruptions started some distance before my collecting spot. At 7:41 p. m. the queen reached the observation point and was taken. She was accompanied by a small retinue of workers with only ten to 20 majors included in the retinue itself and among the guard workers one meter in front and behind the queen. At 7:45 p. m. the last brood passed the observation point, and at 7:51 p. m. the last worker passed. More Phoridae were again noticed near the end of the emigration column, and one passed after the last ant went by. Observations were continued for five minutes after the last ant passed, and then I followed the emigration trail in the direction of the old bivouac without finding any more ants or myrmecophiles. Between 8:00 and 9:00 p. m. there was a raid column extending in the direction approximately opposite to that from which the ants had emigrated to the present bivouac. No backtracking column had started by that time, but by 4:00 a. m. the following morning (5 July 1956) there was a column about one ant wide along both this new raid route and the backtracking route. At 8:00 p. m. the colony was found emigrating along a route almost parallel to that used in coming to the bivouac of 4 to 5 April. Backtracking columns were seen along the emigration and raid trails of colony E-204 in the laboratory clearing up until 10 July. These backtracking columns stopped daily about 6:00 a. m. and started again in the evening.

If the above divided emigration had been observed only in the evening, one might conclude that the entire emigration of an exceptionally small colony had been seen. Such "continuation emigrations" are rather common for *Neivamyrmex nigrescens* (Schneirla, 1958) but have not been reported for the epigaeic *Eciton* species except in cases where emigrations are interrupted by rain. Perhaps all subterranean army ants frequently have divided or continuation emigrations. Before colony E-204 was studied, colony E-143 had been found on 11 April 1956 at 7:30 p. m. while it had only a weak raid column. Between 7:30 and

8:00 p. m. there was a gradual shift to an emigration. At 8:30 p. m. the queen was taken as she was running along in a small retinue, and by 8:35 p. m. the last ants had passed the observation point. If this short emigration included an entire colony, it clearly was the smallest colony which I have ever seen for any species of army ant and must have comprised between 30,000 and 60,000 workers. However, the finding of the divided emigration of colony E-204 strongly suggests that during the preceding night colony E-143 may have started an emigration which was interrupted. Rain did not delay or interrupt this emigration for no rain fell during the entire preceding week. In addition, other facts indicate that the colony was following a strong chemical trail previously used either by a raid or emigration column. The raid column of colony E-143 advanced quite rapidly over the forest floor, and within a half hour the column changed into a strong emigration column. At the time the raid column was found the ants had not yet advanced across several meters which were used by the emigrating ants a half hour later.

The other two emigrations of *dulcius crassinode* which were observed (colonies '55 D-1.Mar. and E-137) were found about 8:15 p. m. after both columns were at their maximum emigration strength. The queens of these colonies were seen on the emigrations between 8:30 and 9:00 p. m. The emigration of colony E-137 lasted until 10:40 p. m. at the observation point; the other emigration was watched only until 9:25 p. m. Both these cases show timing similar to emigrations of *E. hamatum* but probably somewhat later in both their start and finish. The queen clearly emigrates near the end of the colony, and the colony size is probably close to that of *hamatum* on the basis of the meager evidence from the above emigrations.

Bivouacs and Refuse Deposits of *Eciton dulcius*

Although a number of columns of *dulcius crassinode* were traced to holes in the ground, pounding on the ground or shallow digging indicated that the bivouac probably was not near the surface. The only bivouac which was located was that of colony E-204 which was partially dug out at 7:45 a. m. on 4 July 1956 after the first part of the colony's emigration had been completed. The ants were in a depression which had been filled in by placing limbs of trees parallel to one another. No ants were on the surface when the digging began. Most of the ants were in clusters hanging from

branches five to ten centimeters in diameter. Most of the nearly full-grown larvae were held up in the ant clusters, but many were widely scattered between the branches, under leaves, etc. There was no indication that the larvae were arranged according to size. The colony had columns going into holes which extended at least 30 cm. below the exposed part of the bivouac, but no digging was done deeper than 40 cm. No raid columns were seen throughout the day until a backtracking column started about 5:00 p. m. and a small column extended about 50 cm. in the opposite direction. A few scattered pieces of booty refuse but no distinct refuse deposits were seen. Bruch (1923: 173) reported finding refuse deposits in three peripheral chambers of a leaf cutter ant nest which had been occupied by *dulcius s. str.* In this nest he found workers in upper chambers and larvae and cocoons in two lower chambers. Bruch (1923, 1934b) found that *dulcius s. str.* often bivouacked in abandoned or occupied nests of *Acromyrmex heyeri*, *A. silvestri*, *Atta*, or *Cornitermes*.

Interrelations Among Individuals of *Eciton dulcius*

A total of four queens of *dulcius crassinode* have been taken, and all were removed from emigration columns. The dates and times when these queens were taken are given in table 3. These queens were all kept alive for observations in the laboratory, but like all *Eciton* queens they quickly died. Queen E-137 lived for six and one-half days in the laboratory with over 1,000 workers. This queen drank some water from cotton but never was seen to eat or to be fed by the workers although food was present in the laboratory nest. Queen E-204 lived for five and one-half days in the laboratory with less than 200 workers. All these workers, except for two majors, died before the queen. This result was in marked contrast to other *Eciton* queens from epigaeic colonies which died while most of the workers taken with them were still quite active. Circocyllibanid mites and limulodid beetles were present in the laboratory nests, but there is no clear evidence that the death of the workers was hastened by these myrmecophiles. Samples of workers of the more subterranean species usually outlived their queens taken at the same time, but the workers died more quickly than those of the epigaeic species, *burchelli* and *hamatum*. Workers from colonies of *dulcius* usually died sooner than those of *vagans* in laboratory nests; however, a sample from colony E-212 of *E. vagans* died at the same time as their queen after only three days

in the laboratory. As in the other species of *Eciton*, large workers of *dulcius* usually lived longer than the small workers in the laboratory.

The queen of colony E-143 was placed in an empty nest 20 cm. square, and the nest was connected by a tube to a larger nest containing almost 3,000 *dulcius crassinode* workers from colony E-137 which had been in the laboratory without their queen for about 13 days. Sixteen workers immediately entered the nest with the queen and alternately climbed on her and ran around the nest. Only two attempted to sting the queen, and none bit or pulled her appendages. The workers readily licked her body and especially her gaster which may have had an excess of secretions or dirt on it since no workers had been with the queen for two days. The tube was clamped shut to prevent additional ants from entering the chamber with the queen. The positions of all workers which licked or kept their heads over a segment for at least two seconds are recorded in table 4. These data are comparable to those recorded with *E. hamatum* and indicate that the workers are more attracted to the first two gaster segments and not to the anal region. None of the workers was attracted to the mouth parts of the queen. After 25 minutes about 60 additional workers were let into the nest, and when some of these started biting and stinging the queen, no further observations were attempted.

Eciton mexicanum Roger

Six subspecies of *Eciton mexicanum* Roger had been described on the basis of differences among the queens and males (Borgmeier, 1955: 250-261). The workers can be referred to a subspecies only on the basis of the locality where they were found or by association with reproductives. Borgmeier has described the subspecies *panamense* based on specimens from Barro Colorado Island and several other localities in Panama. The male of this subspecies is not known. As a result of dividing *Eciton* into several genera, the name *E. mexicanum s. str.* can again be applied to the subspecies discussed by Schneirla (1947) under the name *E. rogeri*. This subspecies is known from Costa Rica and Mexico (Borgmeier, *l. c.*).

Colony numbers were assigned to 31 colonies of *mexicanum* found on Barro Colorado Island from February to August 1956. However, this list probably includes about ten colonies to which two numbers were assigned, since no colony could be followed for its entire emigration. Nevertheless, *hamatum* was the only species

of *Eciton* found more frequently (with 32 colonies recorded). Since *mexicanum* is the smallest species, has the narrowest raid columns, is most timid and is one of the more subterranean and nocturnal of the five common *Eciton* species, one would predict that fewer colonies would be found. The above data may indicate that *mexicanum* is either more abundant than *hamatum* or has more frequent or diffuse raid columns.

Raids of *Eciton mexicanum*

The most common booty seen being carried by *Eciton mexicanum* were larvae and pupae of ants and occasional adult ants. All raid columns except one were found on the ground or on objects close to the ground with little indication that this species raids up on any vegetation. The single exception, a raid column of colony E-135, extended at least six meters up a tree trunk, and numerous white larvae about 15 mm. long were being carried down the trunk between 8:10 and 8:40 p. m. On one occasion a colony was found attacking a large cricket more than two centimeters long. The cricket was being actively attacked by about 25 ants, but more than twice that number were standing quietly around the cricket. When a cicada, whose thorax had been crushed to prevent flight but not movement, was placed next to the same raid column, the ants did not attack it even when they touched the cicada. The same species of cicada was killed by *L. coecus*. Other large insects like beetles were not attacked, and the ants ran from them.

Compared with swarm raids or even column raids of *hamatum*, the raids of *mexicanum* are much less spectacular and often difficult to observe because they are hidden under leaves and other objects. Most of the actual attacking goes on underground in ant nests. The rate of progress for a large raid column was five meters in a half hour (between 8:45 and 9:15 p. m.). The same colony, E-151, also had two much shorter and less active columns branching from the base column. These branch columns and a number of other raid columns of other colonies advanced at a rate of about six to eight meters per hour. The distal ends of the raid columns of *hamatum* usually have small groups of workers which fan out slightly and sometimes look like miniature swarms of ten to 50 workers. However, the advancing columns of *mexicanum* show much less branching at their tips, often giving the distinct impression that the workers are following a narrow chemical trail. The fans at tips of columns sometimes were five to ten centimeters wide. Even after a chemical

trail must have been well established by at least several hours use, the tendency to stay under fallen leaves was more pronounced than that shown by the other species of *Eciton*. When the leaf cover was removed, the column shifted a few centimeters to adjacent leaf cover. The smaller size of the workers of *mexicanum* would appear to be an advantage in raiding under objects. The majors are two to four millimeters shorter than those of the other four species of *Eciton*, and the other *mexicanum* workers are proportionately smaller. The shifts of columns occurred at night when the only light was from a flashlight. Air currents or some other factor may also cause such shifts. No measurements were made of light intensity, but *mexicanum* was more easily disturbed by light and attempts at collecting than any of the other species of *Eciton*. For example, a drop of saliva three millimeters in diameter caused a complete break in a steady raid column. The ants ran in opposite directions away from the drop but quickly resumed travel along the column with hesitation at the drop. Without any visible interference with a raid column, there were frequent fluctuations of traffic moving in both directions, and at times there would be gaps of a meter or more with no ants on the trail between spurts of activity.

Twenty-eight raid columns of *Eciton mexicanum* were found on Barro Colorado Island between the hours of 6:00 p. m. and 1:50 a. m. The only colony which was not found raiding at night was colony E-184 observed between 2:45 and 4:30 p. m. on 4 June 1956. Throughout the literature on various species of army ants there are many statements that these ants appear after rains. This case of a diurnal raid of *mexicanum* followed a rainfall of 1.6 inches on 3 June and one of 0.26 inches on 4 June. On both days the rain was concentrated around midnight when it might have interfered with raiding. May was a moist month with 16.55 inches of rain, but the last rainfall of an inch or more before 3 June was on 23 May. The lack of more afternoon records is perhaps due primarily to less field work at that time; however, extensive field work was done in the morning without revealing a single raid of *mexicanum* after dawn. The only exception to the total lack of epigaeic activity during the morning was a backtracking column of colony E-108 on 15 February 1956 in the early dry season. This column was found at 11:30 a. m. along the route of the emigration of the previous night. The column was a steady one, but the ants were scattered six to ten centimeters apart and were almost all under leaves. This column would not have been found if I had not known exactly where to look, since

only an occasional ant could be seen without removing leaves. Likewise, considerable numbers of raid columns of *mexicanum* probably escaped notice because they were hidden under leaves.

Four raids were found between 6:00 and 7:00 p. m., and perhaps these were initiated near the time when the epigaeic species are beginning their afternoon resurgence following the siesta period. Since some nocturnal raid columns were weak but increased in strength while they were watched, it is probable that many raids are started after dusk.

In southern Mexico two column raids of *mexicanum s. str.* began within two hours after dawn, and all raids were "reduced to a minimum through the midday hours" (Schneirla, 1947: 5-6; pers. com.). These ants were observed during the dry season, but they were fairly actively raiding throughout the day, and nocturnal raiding was not mentioned.

Although the epigaeic species, *hamatum* and *burchelli*, have been distinguished on the basis of their raiding and other behavior from the remaining species of *Eciton*, there has been no attempt to arrange the species within the subterranean group according to their behavior. Referring to all the subterranean species, Schneirla (1957a: 125) states: "These, although at times found in surface bivouacs under humid conditions in deep forest, at times carrying out full column raids on the surface, are persistently subterranean in nesting and often make extensive use of underground avenues in their raids and emigrations." Although workers carrying booty frequently can be followed back to holes in the ground, there is no good evidence as to how extensive the underground raid or emigration trails might be. On the basis of the large amount of nocturnal activity and the greater tendency for *mexicanum* to stay under leaves in its raiding, I would rank *mexicanum* as "more subterranean" than *vagans* and *dulcius*.

Colony E-197 had a raid column in the laboratory clearing which carried booty into the same hole between drainage tiles which had been used five weeks earlier by an emigration column of *Neivamyrmex pilosus*. Although these tiles and the foundation of the building limited the number of holes available, there were other holes and cracks in the vicinity. No other example is known in which *mexicanum* may have been following another army ant trail.

Emigrations of *Eciton mexicanum*

Six emigrations of *Eciton mexicanum* were watched on Barro Colorado Island for the following periods: 4 hours, 2 hours, 40,

15, ten, and five minutes. The earliest emigration was that of colony E-170 found at 6:20 p. m. At that time less brood was being carried, and the column was slightly narrower than it was about 7:00 p. m. when the column reached its maximum width. Therefore, this emigration was probably seen within an hour of its start. Schneirla (pers. com.) observed one emigration on Barro Colorado Island that began its consistent exodus about 6:00 p. m. with the queen emigrating about 8:00 p. m. The latest observations of emigrations were made on colony E-108 which still had a strong column at 11:35 p. m. about two hours after the queen had reached the observation point. This colony was found at 9:30 p. m. when the emigration column was at its maximum strength, and within ten minutes the queen was seen. Perhaps she emigrated relatively early rather than after 75 to 90% of the colony had left the old bivouac. Schneirla (1947: 5) found an emigation of *mexicanum s. str.* at 5:30 p. m. during the dry season in southern Mexico.

Emigration columns like raid columns were normally found on the ground under leaves. However, on one occasion an emigration followed a slender liana which started at the ground and extended about 70 cm. above the ground at its maximum height. The ants followed this liana for more than two meters. The diameter of the liana was approximately five millimeters, and for most of its length the ants had made a flange ten to 15 mm. wide. Within the flange there were numerous *mexicanum* larvae, but it is not known whether they were feeding there.

Like the raid columns, the emigration columns of *mexicanum* were more easily interrupted than those of the other species of *Eciton* commonly found in Panama. When we were trying to collect workers or myrmecophiles with forceps or aspirator, an emigration column frequently stopped completely with the ants running back toward the old bivouac. Light would also cause more disturbance of the column than was exhibited by emigrations of other species of *Eciton*. However, even when the light was kept constant and no collecting or other noticeable disturbance of the column was made at the observation point, the number of ants along the column varied more than was seen in other emigrations of *Eciton* except for one emigration of *dulcius*.

If one gently brushed the edge of the emigration column with forceps, major and intermediate workers including both guard and emigrating individuals would attack the forceps. Soon a group of six to ten workers would form a ball at the tip of the forceps, and

this response could be facilitated by holding a worker at the tip. That worker evidently released some chemical which would arouse the other ants even without actual contact. Other species of *Eciton* reacted in a similar manner; however, only between three and five balls of *mexicanum* workers could be collected at one place along the emigration column; whereas many repeated collections of the more epigaeic species could be made. The workers of *mexicanum* would fan out on the ground like other species at the site of the disturbance, but then they would break the emigration column completely with workers running in opposite directions away from the disturbance.

No good estimates of the size of *mexicanum* colonies are available. Based on the partial emigrations observed, one would predict that the colonies are about the size of those of *hamatum*.

The only evidence available supporting the hypothesis of a nomadic-statary cycle is the type of brood seen in emigrations in Panama and Schneirla's observations on the broods in bivouacs in Mexico. (More details on the latter are given below under the section on bivouacs.) No eggs or cocoons have been taken from any emigration column. Colony '45 K studied by Schneirla (1947: 5-6) in Mexico had a "single brood of well-advanced worker larvae" and emigrated on two successive nights. Four colonies, E-108, E-170, E-251, and E-256, all had broods of larvae with a total range in lengths of 1.2 to 7.6 mm. Callow workers were seen in the emigration columns of these four colonies and also those of colonies E-153 and E-239. As among other species of *Eciton*, callows of *mexicanum* were more likely to be carried in the emigrations than older workers. Judging from the callows seen in colonies which had some larvae between 6.0 and 7.6 mm., the smallest workers emerge last. At times when only slight differences in color could be distinguished among the majors, the smallest callow workers were a light yellow straw color contrasting conspicuously with the dark red-brown older adults. The range in color indicates that the workers of *mexicanum* emerge through a longer period than those of *hamatum* and possibly longer than those of *burchelli*. The three queens taken from emigration columns and the previous queens reported by Schneirla (1947: 5-6), Bruch (1934a: 125-127) and Borgmeier (1933: 96; 1955: 250) were all contracted when found. The lack of cocoons, presence of callows, presence of contracted queens and synchronous broods on emigrations all indicate that *mexicanum* has a nomadic-statary activity cycle comparable to *hamatum*.

On all emigrations there was a noticeable increase in excitement when the queen ran along the column, however, the retinues of workers were relatively small. On the emigration of colony E-170 there was no clear retinue even though the queen was not moving unusually slowly or quickly. Perhaps my disturbance of the column for about four hours before the queen passed had attracted most of the majors from the bivouac to my observation point. Most of the majors were not collected because it was impossible to do so without interrupting the emigration, and the majority had gradually moved toward the new bivouac. For at least an hour before the queen reached the observation point, between ten and 14 majors were constantly present as guards along the edges of the column. Although these majors did not have any direct contact with the queen as she passed, they reared their bodies upward and waved their front legs and antennae more quickly. The column did not widen and no ants rode on the queen. The other two queens were accompanied by more distinct retinues, but my collecting made it impossible to get an estimate of their normal size. The queen of colony E-251 was found running toward the old bivouac in the opposite direction of the retinue. This was probably due to effects of my light, since I had been collecting at this spot for only five minutes. The wave of excited workers making up the retinue passed on toward the new bivouac with no indication that the queen was not among the workers. The queen was collected before any of the majors or other workers could gather over her.

Bivouacs of *Eciton mexicanum*

Only a single bivouac of *Eciton mexicanum*, colony E-184, was located during this study in Panama, and it was under the base of a tree where it was impossible to dig it out. The ants entered next to a buttress root, and a small cluster was within five centimeters of the surface of the ground. Pounding on the surrounding ground and pushing sticks down cracks caused several thousand ants to pour out of the bivouac. The raid columns had only dark workers on them; nevertheless, a large number of callow workers came out of the bivouac when it was disturbed. Unfortunately no brood was found although 1,522 workers were taken. Since callows were not participating in the raids to any extent, and since no larval brood was seen, this colony probably had just started a nomadic phase.

Schneirla (1947: 5-6) reported finding in Mexico one statary bivouac of *mexicanum s. str.* inside a hollow log and another well-

hidden bivouac in the remains of an old tree root hidden under vines and detritus. In Costa Rica a bivouac of the same subspecies was found by Nevermann under wood on the ground (Borgmeier, 1933: 96). In spite of much more extensive studies of army ants on Barro Colorado Island by Schneirla and others, no bivouac of *mexicanum panamense* has been found which was as exposed as those from Costa Rica and Mexico. Perhaps these two subspecies have differing ecological preferences for bivouac sites, or the exposed bivouacs may have been found by chance in more moist places.

Other Species of *Eciton*

The remaining species of *Eciton* are either rare or absent in Panama. Only brief comments or additional records are given for comparison with the other species. Omitted are two remaining species, *E. setigaster* Borgmeier and *E. uncinatum* Borgmeier, known only from a few males.

Eciton quadriglume (Haliday)

Borgmeier (1955: 199) has reported that *Eciton quadriglume* ranges from Misiones Province, Argentina northward to Peru and the state of Amazonas in Brazil. However, he also reports examining a specimen with the locality "Panama" (p. 198). Although the species of *Eciton* in Panama rarely or never attack *Atta* and other leaf cutter ants, *quadriglume* apparently attacks these ants frequently (Reichensperger, 1924b). The bivouacs may be either epigaeic or subterranean. The males seem to be produced over a longer period of time than those of most species of *Eciton* and have been found during both rainy and dry seasons on dates from November to May (Borgmeier, 1955: 199-200; and my collection).

Eciton rapax F. Smith

Eciton rapax is a rare species known only from the workers found in central and northern Brazil, Bolivia, Peru, and Colombia. Borgmeier (1955: 212) considers that *E. jansoni* is probably the male of *rapax*. *E. rapax* is of special interest because majors with hook-like mandibles have never been found even though large workers 13 mm. in length have been taken.

Eciton jansoni Forel

Eciton jansoni is known only from a few males taken in Nicaragua, Costa Rica, Panama, Colombia, and Equador (Borgmeier, 1955: 212). Borgmeier has considered this species to be the male of

rapax. Because the distribution of *jansoni* extends much farther to the north overlapping that of *rapax* only in Colombia, it is more probable that *jansoni* is the male of *dulcius crassinode*. If this association can be proved, *crassinode* would become a synonym of *jansoni* which would remain a valid species. Males of *jansoni* have been taken from February to June, and thus, seem to be restricted to the dry season and early rainy season. Only two records are known from Barro Colorado Island: 31 May 1956 (C. W. and M. E. Rettenmeyer 1891) 1 ♂ taken at light, and May 1941 (J. Zetek 4800) 1 ♂. (I have not seen the latter specimen, but it is recorded under the name *E. velutatum* in the catalog of species found at the Canal Zone Biological Area.)

Eciton drepanophorum F. Smith

The only observations of the behavior of *Eciton drepanophorum* were made by Bates (F. Smith, 1858: 149; Bates, 1863, vol. 2: 356-357). Judging from these observations *drepanophorum* may be as epigaeic as *hamatum* since it attacks wasps and drives insects in advance of its raids. It may have swarm raids, because Bates reported ant birds accompanying its raids.

Labidus praedator (F. Smith)

Labidus praedator ranges from central Mexico (state of San Luis Potosi) south to northern Argentina and is one of the most common species of army ants throughout its range. Borgmeier (1955: 111-113) has divided *praedator* into two subspecies (*praedator s. str.* and *sedulus*) which seem to be sympatric from Bolivia to Costa Rica. A few records indicate that the two subspecies are not ecologically separated according to elevation. Even though the species is common, the males have not been adequately collected to show the exact distribution of either subspecies. Workers were referred to these subspecies by Borgmeier (*l. c.*) on the basis of the shapes and sizes of the heads of major workers. However, these distinctions are difficult to see and of little value since there is no known way to determine which workers are the largest in a colony without collecting the entire colony. There does not seem to be any distinct morphological change between majors or soldiers and submajors such as occurs in *Eciton*. In addition, one can seldom collect the largest workers present in a colony since these never or only rarely take part in the raids. Borgmeier has referred all specimens from Barro Colorado Island to *praedator sedulus*

Menozzi. The largest head width reported for workers (soldiers) of this subspecies is 2.8 mm. compared with 3.4 mm. for *p. praedator*. However, the largest workers we found on Barro Colorado Island have head widths under 3.0 mm., and the largest workers commonly seen have heads only 2.0 to 2.5 mm. wide.

The workers of *praedator sedulus* all have strong bites, and even the smallest workers could bite my skin more severely than workers of comparable size belonging to any other species of army ant found on Barro Colorado Island. However, the stings of the *praedator* workers in most cases could not penetrate my skin.

Raids of *Labidus praedator*

Labidus praedator eats different species of ants but never was seen attacking or carrying *Paraponera clavata*. Like *E. burchelli, praedator* appears to feed on a wide variety of arthropods, and Schneirla (1949b: 75) has reported that it feeds more on smaller organisms than does *burchelli*. Although a quantitative study has not been made, it is likely that *praedator* kills almost all the arthropods killed by *burchelli* on the forest floor, but less frequently kills the larger species such as scorpions. The minor workers of *praedator* are especially numerous and much smaller than the minors of *burchelli*. These tiny workers probably attack minute ants and possibly Collembola and mites. However, only a few mites (Oribatei) which appeared to have been bitten by ants have been found in samples of *praedator* taken from raids. Williams (1941: 116) reported that the minimal numbers of microarthropods which he recovered from forest floor litter were found in the two areas raided on the previous day by army ants, identified as *praedator* by Schneirla (1956b: 391).

If one judges from the recognizable booty in raid columns, ants are the most frequent prey. During 1956 we observed *praedator* also killing numerous other arthropods including: Isopoda, Amphipoda, Araneida, and Orthoptera (Gryllidae, Tettigoniidae, and Blattidae). It was seen to attack Scarabaeidae and Histeridae but abandoned these beetles after a few minutes with little damage to the beetles.

Like other army ants, *L. praedator* will attack vertebrates but seldom kills them. I have never seen this species feeding on any vertebrate, but Reh (1897: 615) reported finding a mouse covered with *praedator*. The mouse was still twitching and was bloody from the attacks of the ants, but it was not stated whether the ants actually stripped any flesh from the mouse.

Borgmeier (1955: 108) has given a brief review of unusual foods which *praedator* has been reported to eat or carry. Included are carcasses of dead animals, sugar, crushed pineapple fruit, boiled rice, palm fruit (*Attalea indaya*), and dried apple cuttings. It is not clear how many of these items the ants were actually eating and how many may only have been carried. In addition, the ants may have been attracted to these substances because of moisture on them; in fact, workers will readily lick and sometimes carry a small stick or other object which is moistened with water. *Labidus praedator* was found clustered more frequently than any other army ant on moist spots on the forest floor where leaf litter had been scraped away or where water was spilled. This ant was also seen drinking droplets of dew on grass at night. In laboratory nests *praedator* would not eat peanuts, and I have found no reports of its eating vegetable oils of any kind. In marked contrast, *L. coecus* frequently eats these types of plant materials.

The raid swarms of *praedator*, like those of *burchelli*, are not as successful as one would conclude from the literature. Sometimes *praedator* entered the nest of a potential prey ant but would be successful in capturing only a few individuals. Most workers of the attacked species which ran out of their nest carried larvae or other brood and often escaped by running up vegetation where the *praedator* did not find them. *L. praedator* also did not cover the ground thoroughly, and numerous insects could stay quietly between anastomosing columns until the swarm raid had left the area. When a swarm raid of *praedator* did attack potential prey, it was amazing how quickly this small army ant could remove legs and tear up many arthropods. In a few seconds the army ants could remove all the legs from a cricket and have started pulling the rest of the body apart.

The basic pattern of a swarm raid of *L. praedator* is similar to that of *E. burchelli* during the first half of a morning raid; however, there are a number of significant differences. The raids of *praedator* at corresponding stages are usually considerably smaller than those of *burchelli*, and the swarm front seldom exceeds four meters in width. A maximal swarm raid of *praedator* is about eight meters wide at the swarm front and has the same general shape as the swarm raid diagrammed for *burchelli* in figure 6. However, during the 1956 work in Panama it was evident that maximal raids do not occur frequently, and when they do occur they may show the maximal development only a brief time. We never found a swarm

raid of this species which lasted for several hours in the typical pattern of a *burchelli* swarm raid.

Wheeler (1921: 310-311) stated that raid columns of *praedator* are conspicuously broader and denser than those of other army ants. This would apply only to *praedator* raid columns of maximal size which are dense ribbons of ants about ten ants wide. Raid columns of this width occur also during maximal raids of *burchelli*. However, the raid columns of *praedator* which are most frequent are one to three ants wide.

Since the bivouacs are typically subterranean, it is usually impossible to find their exact location by following the workers carrying booty. When workers carry booty away from the swarm front, they may enter holes in the ground in five or more places only a few meters apart. As the raid progresses, new holes are used, and some of the olders ones may be abandoned. The ants are constantly raiding on, or at least extending, underground trails at the same time as the ants advance on the surface. Many of the holes used are not more than one to three meters back from the swarm front, and thus the fan area of anastomosing columns is not as extensive as that of *burchelli*. A base column may be completely absent on the surface of the ground, but the steady flow of ants in and out of holes near the swarm front indicates that there is a continuous column to the bivouac. On several occasions base columns along the surface of the ground have been followed for more than 100 meters. Booty was seen being carried in one direction for the entire length of these long epigaeic columns. Ants carrying booty along the more common epigaeic raid columns which extended only one-half to three meters often carried booty in opposite directions on two columns. The shifting of columns used by the booty carriers and the conflicting directions of the traffic add to the difficulties of trying to locate the direction of the bivouac. As the swarm advances much booty is temporarily put in caches under leaves. The booty may be carried back toward the bivouac for at least two hours after the swarm raid has stopped. During this period hundreds of workers can often be found standing under leaves apparently doing nothing, and essentially no additional prey is attacked after the swarm raid stops.

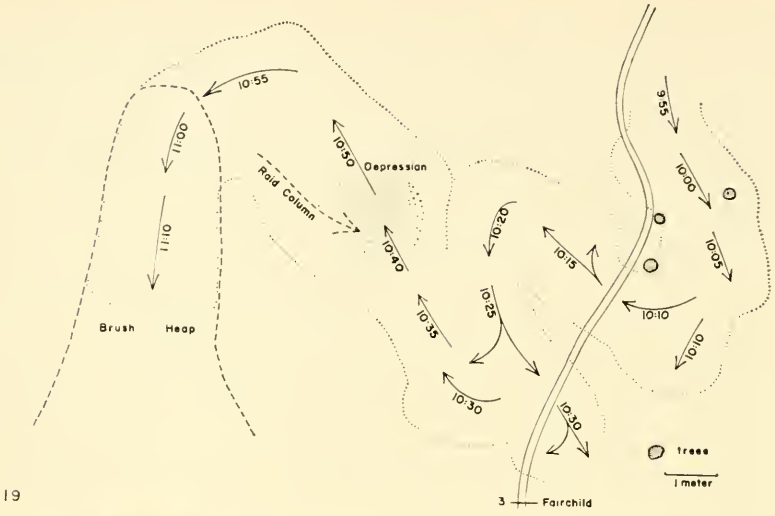
When *praedator* raids subterranean ant nests, one would expect that much of the booty would be carried back to the bivouac along subterranean routes extending from the passages of the raided nest. Perhaps this is not the case since the majority of booty being carried along the epigaeic trails and seen in the booty caches is brood of

other species of ants. At no time was brood of *praedator* found in any of the booty caches; however, there was only a single case where a raid column changed into an emigration column while it was being watched. Since most larvae of *Eciton* which are found in booty caches are dropped there only after the beginning of an emigration, one would not expect *praedator* larvae to be found in booty caches along raid columns.

Maximal raids of *praedator* may continue in approximately the same direction for more than 25 meters with a pattern similar to figure 6. However, it is more frequent to find the swarm raids of *praedator* shifting their direction. The smaller swarm raids usually were the ones which showed the greatest tendency to change direction. In a similar manner small swarm raids of *burchelli* were diverted more sharply to one side or the other. Typical diagrams of two partial swarm raids of *praedator* are shown in figures 19 and 20.

The swarm raid of colony E-230 shown in figure 19 was found at 9:55 a. m., and the ants were advancing rapidly without finding a noticeable amount of booty. During the one and one-quarter hours that this swarm raid was observed the ants made four major shifts in direction. The fine dotted line indicates the maximum extent of the ground covered by the ants. Each arrow shows the position of the swarm at the time indicated with the swarm front near the head of each arrow. In addition to the major shifts, there was constant irregular back and forth shifting within the width of the swarm front. Three small trees may have influenced the direction of the swarm raid to some extent, but other trees within the area raided had no visible effect on the path of the ants. (These other trees are not shown in the diagram.) The abundance of booty may be one of the most important factors influencing the direction of these raids. Since a high percentage of the booty was hidden in caches under leaves, it was difficult to determine the source of most of the booty.

In two areas shown in figure 19 the progress of the ants was slowed. The stippled depression shown in the center of the diagram was entered by ants about 10:40 a. m.; and even though many ants continued beyond it at 10:50 a. m., other ants raided there extensively during the next half hour. The moist leaves in this depression may have attracted the ants as much or more than booty found there. The brush heap outlined by the broken line at the left of the figure also slowed the progress of the ants while



19

20

FIGURE 19.—Path of swarm raid of *Labidus praedator*, colony E-230, from 9:55 to 11:10 a. m., 31 July 1956. Swarm raid at any time was similar in shape, but much smaller than in figure 6. Each solid arrow indicates direction and time for majority of advancing ants. Dotted lines show maximal extent of swarm fronts. Dashed line labelled Raid Column is major route along which ants carried booty into a depression. (Bivouac site unknown, not in brush heap or depression.) Parallel lines indicate Fairchild Trail from station 3.0 to about 3.1. Dashed line on left shows edges of large brush heap in which raid could not be followed. All trees are indicated which were close to edges of raid and may have influenced its spread; other trees in main body of raid or farther outside not indicated. Area sloped downhill toward left.

FIGURE 20.—Path of swarm raid of *L. praedator*, colony E-220, from 10:00 a. m., to 12:30 p. m., 25 July 1956. Ants carried booty primarily along four columns to holes labelled A, B, C, and D at times indicated. Parallel lines show Barbour Trail between station 5.1 and 5.2. Area almost level.

thousands of workers dispersed upwards into the tangle of branches, vines, etc. At 11:10 a. m. the advance of the ants could no longer be followed because of the difficulties of working in this tangle of vegetation. There were at least five temporary columns along which booty was seen carried, but only the last one observed is indicated in the figure. Colony E-230 may have shifted its raiding toward the west due to the downward slope of the ground in that direction. The David Fairchild Trail follows a contour line at that spot, and the ants moved parallel to it at first. About 10:15 a. m. they moved directly down the slope; but around 10:25 a. m. the swarm had a distinct fork, and part of the ants moved up the hill to cross Fairchild Trail again, and part of the ants turned down the hill. Raids of other colonies show similar patterns indicating that the slope of the ground is of much less importance than the amount or type of booty or the vegetation cover for influencing the direction of the raids of *praedator*.

The swarm raid of colony E-220 diagrammed in figure 20 was found at 10:00 a. m. on 25 July 1956 while the raid was moving southward across a fairly level area. In a few minutes a noticeable shift in traffic started toward the west, and it soon became clear that this was the main direction that the swarm was heading. For no discernible reason the ants decreased on the southward movement, gradually stopping all advance in that direction shortly after 10:30 a. m. In a few places it appeared that trees may have influenced the direction of the ants, and these trees are indicated on the figure. After almost an hour in which the ants raided primarily toward the west, they shifted more toward the north. By 11:00 a. m. it was clear that the raid was slowly decreasing in strength. The workers decreased in number and seemed to be moving more slowly. Shortly after 11:00 a. m. it became difficult to distinguish a swarm front or any area where the ants were actively advancing. After 11:15 a. m. almost all the ants were tearing up booty previously caught, carrying booty back along trails, running along trails without booty, or just standing quietly.

The primary trails used by ants which were carrying booty are indicated by the broken arrows in figure 20. The first one labelled A was used extensively between 10:00 and 10:30 a. m. with subsequent traffic decreasing until about noon. Since this trail went almost due south, one might think the bivouac was in that direction. However, about 11:30 a. m. the next column used had ants carrying booty toward the northwest, and traffic on the subsequent columns

went south and southeast. Around noon all four columns had ants on them carrying booty into the respective holes. When the ants retreat into a hole in the ground, the end of the raid column is quite similar to the end of an emigration column of *Eciton*. The last ants on the column run back along the trail in a manner almost as hesitant as that of the ants which are advancing the swarm front.

In the upper left part of figure 20 it can be seen that the ants completely reversed their direction of progress and doubled back over much of the same area previously raided. This reversal of movement or circling back over the same area results from a continuation of the more zigzag manner of raiding by *praedator*. Parts of a swarm raid of *burchelli* may circle back over the same area raided only a few minutes before, but such a route is much more distinct with *praedator* since the entire swarm raid or most of it is included.

Labidus praedator probably raids extensively underground, judging from the number of columns which enter and come out of holes even where there are no ant nests which are being raided. This army ant also raids under leaves more than the five species of *Eciton* observed, with the possible exception of *E. mexicanum*. The smallest workers, about two millimeters long, can be seen running into holes and cracks which are much too small for the largest workers. Like other army ants, *praedator* digs readily and will enlarge holes until the larger workers can go through them.

In addition to its subterranean raiding, *praedator* also raids up trees and buildings. However, this army ant usually went only about two meters above the ground and never was seen to go higher than three meters. When *praedator* raids in low shrubs and trees, it does not cover the vegetation as thoroughly as does *burchelli*.

Seventeen *swarm* raids of *praedator* were found at various times throughout the day between 9:00 a. m. and 10:10 p. m. Although swarm raids probably occur at all times of the day, the data are inadequate to determine whether there is a tendency to have raids during any particular period. Raid columns were found at all hours of the day and night. The more frequent appearance of *praedator* either during the rainy season or after rains has been known for many years (Sumichrast, 1868: 40; Ihering, 1894: 381-383) and was supported by Schneirla's observations in Mexico and Panama (Schneirla, 1947: 10-11). Based on the amount of time we spent searching for army ants during 1956, swarm raids of *praedator* were seen at least twice as often during the rainy season as in the dry season.

In view of the fact that *praedator* is found more frequently during the rainy season, one might expect that the ants would have a siesta period or would never raid between noon and 3:00 p. m. However, we found two maximal swarm raids between noon and 3:00 p. m. in the middle of the dry season during February and March. Moreover, other raid swarms stopped advancing at different times during the day without any obvious connection with environmental factors, except in the case of heavy rains which would halt all raiding activity. Probably a colony has a number of small epigaeic raid swarms during each 24 hour day. These may be widely separated without any epigaeic connecting columns. Adjacent raid columns of *praedator* were found on only one occasion in 1956, and these were considered to belong to two colonies (E-182, E-183) since no connection between them could be found.

Many arthropods were driven in front of the swarm raids of *praedator*, and flies were invariably abundant over diurnal swarm raids but absent over the nocturnal ones. These flies are the same species or closely related to the species of Tachinidae and Conopidae which accompany the swarm raids of *burchelli*. The ant birds were present near some of the larger diurnal swarm raids, but they were more frequently absent, probably because of the small size and short life of most *praedator* swarm raids.

Emigrations of *Labidus praedator*

Emigrations of *Labidus praedator* have been seen infrequently, and no queens have been taken from emigration columns. During 1956 we found two columns which appeared to be emigrations, but in both cases only a small part of the colonies must have been seen. The first case was colony E-177, first seen at 7:10 p. m. on 29 May 1956 when it had a raid column carrying booty into a crack in a concrete drain. This column may have been the start of an emigration since at 6:45 a. m. the next morning there was a much stronger emigration column along the same trail. The column in the morning was considered to be an emigration column since there were myrmecophiles running in it, numerous guard workers were present along the margins, and the traffic was strong and consistently moving in one direction. The column was continuously three to five ants wide, well below the maximum strength of about eight ants wide for emigrations of *praedator*, and no brood was seen being carried. At 7:57 a. m. there was a complete break in the traffic at some underground point toward the old bivouac. When the traffic stopped, all the guard workers immediately left their posi-

tions and moved toward the new bivouac. The column resumed after an interruption of five minutes and quickly regained its former strength. Within the next half hour a few guard workers lined up along the route but not as many as had been present earlier. The column continued at the same strength until rain interrupted it between 9:40 and 9:45 a. m., including three minutes of heavy rain when no ants were seen. When the shower stopped, the column again continued; however, about 10:00 a. m. the traffic decreased to half its previous strength. During this period the sun was becoming stronger, and by 10:30 a. m. the column was partially in bright sunlight. The ants continued to emigrate at an estimated rate of 300 to 500 per minute which was somewhat less than half their previous maximum. Between 10:50 and 11:00 a. m. the sunlight reached its maximum brightness, and the ants stopped emigrating completely. Several myrmecophilous millipeds and possibly 100 workers were seen to enter the area where the sun was shining brightly on the trail, and then they turned and ran back toward the old bivouac. The ants did not continue this emigration in the evening of the same day. However, they may have emigrated later that night because they were never seen again.

This emigration column of colony E-177 extended only about four meters on the surface of the ground. The total emigration distance probably was much greater, but neither the locations of the bivouacs nor other columns of *praedator* could be found in the vicinity. The first meter of the column closest to the old bivouac went through grass, and walls of loose dirt had been constructed for stretches of ten to 20 cm. along both sides of the column. The workers piled moist dirt particles up to make these walls and probably did not add any substance to the dirt to hold the particles together. There were a few places, including one almost 20 cm. in length, where a complete tunnel of dirt had been constructed. Figure 21 shows the walls of dirt and a short stretch where there is a complete roof connecting the walls. Guard workers were standing along the inner surfaces of these walls with their heads facing out along the open top edges. In some short sections the workers formed a partial or an entire tunnel with their bodies. Occasionally a worker could be seen to add a piece of dirt to the walls, and when a short stretch of the wall was broken down, part of it was immediately replaced. This species of army ant has also been seen to make tunnels and walls of wood fragments (Calvert and Calvert, 1917: 307-308).

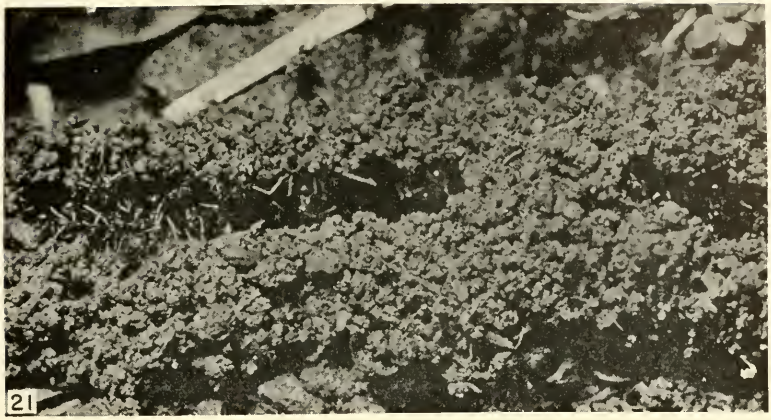


FIGURE 21.—Walls of loose dirt and complete tunnel (near right side) made by *Labidus praedator*. Legs and other parts of "guard workers" can be seen between walls. Main emigration column between walls cannot be seen. (Colony E-177, 30 May 1956.)

It is not clear why the walls or tunnels were constructed in some places and not in others. In the three cases known to me the walls were made along the section of trail where the ants left a subterranean route and started an epigaeic one. Although the type of soil looked identical along the trail immediately following the dirt tunnel made by colony E-177, there was neither a tunnel made up of workers nor an increase in the number of guard workers at any time. In contrast to our observations, Calvert and Calvert (*l. c.*) reported there were many more guard workers which formed walls and a tunnel with their bodies along the column where the dirt tunnel was absent.

An emigration of part of colony E-183 was observed, but the traffic several times moved in the direction of the old bivouac or was equally divided toward the old and new bivouacs. The colony either failed to emigrate or it emigrated by a different subterranean route rather than by the first epigaeic route. The shifting traffic was similar to that seen along columns of *Eciton* when colonies are dividing. At the same time that the emigration column was observed there were several raid columns near by which were not connected with the emigration column, and booty on these was being carried to holes more than 25 meters away from the emigration column. Perhaps all these columns belonged to the same colony, but the raid columns were considered a separate colony (E-182). At 6:45 a. m. on 3 June colony E-183 continued its raid along the same trail from a bivouac probably located at the edge

of the laboratory clearing near the dock. This colony raided throughout the day around the laboratory buildings with increasing numbers of ants moving up the hill and going under the foundation of the old laboratory where small clusters could be seen at the northwest corner during the evening. The ants actively raided through the most open parts of the clearing during the entire day which was cloudy. Between 11:00 p. m. and midnight 1.51 inches of rain fell, and most traffic along the column must have been interrupted. By 1:00 a. m. on 4 June the rain had ended, and at 2:45 a. m. a strong column was moving up the hill toward the old laboratory. However, all booty except an occasional piece was still being carried down the hill. Between 7:00 and 7:55 a. m. on 4 June there was a noticeable increase in traffic up the hill, and more than 50% of the booty was being carried in that direction. At this time the colony was considered to be starting an emigration. Similar traffic with occasional spurts in either direction continued on the column until 10:40 a. m. when the column had greatly decreased in strength and observations were interrupted. The morning was predominantly cloudy, but several brief periods of sunlight seemed to cause a reversal in the "emigration" traffic. Myrmecophiles were seen in this column and were most abundant between 7:55 and 8:55 a. m. At 8:45 a. m. a dealate male was found in the column with so many workers clinging to it that it could scarcely walk. It is not known whether the male was emigrating with the colony or whether it had gotten into the column during the night. During the evening of 4 June the activity on this same column again increased and continued throughout the night with the prevailing traffic frequently changing back and forth. On 5 June there was similar traffic on the column, and five larvae 3.2 to 4.0 mm. long were taken. The colony apparently emigrated in a different direction sometime during the night of 5 June since on the following day no *praedator* could be found around the old laboratory or along any of the trails where they had been seen previously. These observations indicate that colony E-183 either did not emigrate or emigrated only a short distance for two nights at a time when there was a larval brood.

Bivouacs of *Labidus praedator*

Bivouacs of *Labidus praedator* are as rarely found as emigrations. Nests have been reported to be found at great depths with openings 50 or more paces apart on the surface (Rengger, 1835, as reported by Ihering, 1894: 330), but no excavations have been made to substantiate how close any part of the bivouac is to these holes.

Three bivouacs were probably located under the foundations of the laboratory buildings on Barro Colorado Island. A third bivouac (colony '52 P-7) was found in a rotten log about 55 cm. in diameter and extending at least 15 cm. into the soil beneath the log. A bivouac of *E. hamatum* (colony '52 H-A) was within a cavity of the same log. The *hamatum* were about 60 cm. from the *praedator,* but when I completely cut apart the log to attempt to collect the brood and queen of the *praedator,* there was little fighting between the two species. No queen was found, but 154 males including a single dealate were seen in the bivouac. (Borgmeier [1955: 83, 110, 113] states that three males were found in this nest. The total found was 154, but only three were sent to Father Borgmeier.) A total of 147 males was taken alive, and many of these subsequently lost their wings in the laboratory even though they were not allowed to fly. The immature brood consisted of eggs, young larvae and cocoons. Eggs were concentrated in three long chambers which were so narrow that it is unlikely that the queen could have laid them there. Cocoons were in the opposite side of the log primarily in one larger chamber, and larvae were scattered throughout the log in many chambers. The adult males were primarily in cavities in the ground, but a few were in the largest holes in the rotten log. When the males were dug out, it was clear that the largest workers were near the males, and these workers became unusually excited as the workers and males were collected. A large part of the bivouac must have been deeper in the ground, and probably the queen was in this section. At the time the bivouac was examined there was no raid column of *praedator* within ten meters of the log.

Bivouacs of *praedator* have also been found in the same stump with a colony of *hamatum* (Schneirla, 1949b: 18), in the same log with a colony of *E. vagans* (Schneirla, 1947: 9), in a log and in a nest of *Solenopsis geminata* (Schneirla, 1947: 9), under a log and in two nests of *Cornitermes* (Luederwaldt, 1918: 57), under a small bridge made of logs and dirt (Sumichrast, 1868: 40), under foundations of buildings, and in abandoned termite nests (Ihering, 1894: 330; Borgmeier, 1955: 108-109).

Colonies of *praedator* probably include over one million workers and possibly are the largest colonies among species of Ecitonini. Compared with species of *Eciton,* there is a much greater tendency for one to underestimate the number of *praedator* workers due to their small size. For example, a circular column of "several hundred" workers actually included almost 2,000 ants as can be deter-

mined from counting the workers in the drawing made from a photograph of the column (Schneirla, 1944a: 7). Based on one sample of 7,550 workers (colony E-146) aspirated from clusters at the edge of a bivouac under the foundation of the old laboratory there are about 15,000 workers per 100 ml. (compared with 3,000 to 6,000 workers of *E. hamatum*). Observations of emigrations and bivouacs indicate that the broods are also immense (Schneirla, 1947: 9), but no estimates have been made.

Sexual Broods of *Labidus praedator*

Only two cases have been reported in which a sexual brood has been found in a colony (Borgmeier, 1955: 109-110). Rev. P. Schwarzmaier found 12 winged males in a bivouac at Campinas, Goias, Brazil, on 12 September 1935. The second case is the one mentioned above in which one dealate male and 153 winged males were found on 19 March 1952 in a bivouac of colony '52 P-7. In addition, there are two cases in which a single dealate male has been found in a column of workers: on 21 October 1905 Fiebrig found one at San Bernardino, Paraguay; and on 4 June 1956 one male was found in colony E-183 on Barro Colorado Island. Males of *praedator* frequently have the genitalia extruded and widely spread when they are found at lights. Since the genitalia of most of the males taken in the bivouac of colony '52 P-7 showed this same condition, the extrusion of the genitalia is probably not dependent upon flight, though it may occur only after a maturation period. No other species of Ecitonini showed such a pronounced extrusion of the genitalia.

In addition to the above records, males were taken at lights on Barro Colorado Island on the following dates (with the number of males in parentheses): 30 March 1955 (2); 31 March 1955 (3); 20 February 1956, 5:00 a.m. (2); 4 April 1956 (1); 26 April 1956 (1); 3 May 1956, 4:30 to 5:00 a.m. (1); 29 May 1956 (1); and 6 June 1956, 5:15 a.m. (1).

Although lights were run nightly until 19 August 1956, no additional males were taken. The above dates extend from 20 February to 6 June 1956 indicating a flight period of about four months starting during the dry season, with an apparent increase in numbers at the beginning of the rainy season. For comparison, the flights of males of *hamatum* and *burchelli* extended about two months (9 May to 4 July and 17 March to 11 May). Borgmeier also stated that the time of male flights of *praedator* is quite irregular, and

the additional dates cited by him for Panama and Costa Rica fall within the period indicated above.

Activity Cycle of *Labidus praedator*

There is conflicting evidence regarding the amount of nomadism shown by *Labidus praedator*. Several authors have stated that *praedator* has permanent nests ("Dauernester") or at least stays in the same nest site for from several months to three years (Ihering, 1894: 382; Sumichrast, 1868: 40; Luederwaldt, 1918: 57-58; and Borgmeier, 1955: 108-109). Several of these cases may be instances where a colony has left a site and subsequently the same species again bivouacked there. On three widely separated dates we have seen bivouacs, or large clusters of *praedator* which could be confused with bivouacs, at the northwest corner of the old laboratory building on Barro Colorado Island. No bivouac sites were ever seen under or close to any of the other buildings in the clearings. It is possible that this one corner was used frequently because water was spilled every day in this area next to the kitchen. The army ants used at least four routes in going to and from this one site. However, Sumichrast (*l. c.*) reported watching *praedator* every day for three months as the army ants were digging under a small bridge made of logs and dirt. In this case the ants were no longer at the site on 30 September, but about four months later a colony reappeared for a short duration. These observations were made in Mexico during the summer months when one might expect the ants to be most nomadic. All our observations in Panama support the hypothesis that the ants migrate frequently but perhaps more irregularly than species of *Eciton*.

The evidence on the degree of synchronization of the broods is similarly conflicting. The most clear evidence for synchronous broods paralleling those of *hamatum* has been presented by Schneirla (1947: 9) for colony X1 which had one large brood of "newly transformed" worker pupae [= young pupae or young callows?] and a second brood of eggs. However, a second colony reported by Schneirla (*l. c.*) appeared to have only a single brood of pigmented pupae close to emergence. Moreover, Schneirla (1957a: 125) has reported that four emigrations of *praedator* have been observed "in which ran tens of thousands of callow workers, with great numbers of unopened small cocoons being carried along." If these last five cases were to correspond to the typical *hamatum* pattern, a second brood of eggs or young larvae should have been present in each colony. It is possible that it could have been over-

looked in each case or the young brood may have been in a different part of the emigration.

In contrast to the above cases of apparently synchronous broods, there are two examples of apparently nonsynchronous broods. Colony '52 P-7 had one brood of alate males, plus thousands of eggs, larvae and worker cocoons. The males must have been produced in this colony since they were winged and there were so many of them. One would expect to find only worker larvae along with such a brood. My sample of the brood was not as extensive as would be desirable to indicate the true proportions of the different ages. However, it includes about 300 eggs, 193 larvae ranging from 4.4 to 6.8 mm. in length, nine cocoons containing worker prepupae ranging from 3.2 to 8.0 mm., and two cocoons containing young pupae 3.2 and 8.8 mm. in length. Thus, mature pupae and callow adults were the only stages missing. The above measurements also indicate that the largest worker larvae did not spin cocoons first as there is a complete overlap in size among enclosed and unenclosed brood.

The latter case is not unique in that Luederwaldt (1918: 57-58) described a bivouac in which there were eggs, larvae 3.0 to 7.0 mm. in length, and light brown pupae 2.5 to 8.5 mm. in length. He also found innumerable empty cocoons 20 mm. long and 7 mm. wide which he thought were those of males, but no males were still in the bivouac. A similar case of nonsynchronous brood will be discussed under *L. coecus* below.

Labidus coecus (Latreille)

According to the interpretation of Borgmeier (1953; 1955: 86) about 20 specific and subspecific names are synonyms of *Labidus coecus*, and he has recognized no subspecies even though he was convinced that subspecific names could be used on the basis of differences shown among three queens. The large number of names used for *coecus* is in part attributable to its range from the southern United States to Argentina. It is clear from examining males from widely separated localities such as Texas, Panama and Argentina that the color and morphological variation found among specimens of *coecus* is considerable and probably at least as great as that shown by other subspecies of Ecitonini considered valid by Borgmeier. In spite of the fact that males of *coecus* are the most common males of Ecitonini found at lights, the males have been found with workers on only two occasions (Borgmeier, 1955: 92). Queens

taken with workers have been reported from four localities: Mexico, Costa Rica, British Guiana, and Argentina.

Colonies of *Labidus coecus*, like those of *praedator*, appear to have semipermanent nests, judging from one colony which occupied an abandoned termite nest and the soil below it for more than four months (Ihering, 1912: 228). Wheeler observed *coecus* on numerous occasions in Texas but could not find a bivouac. Brues (1901: 353) reported finding one bivouac in Texas which "extended under stones for a distance of nearly twenty feet. . . ."

No bivouac of *coecus* has been found on Barro Colorado Island, and the bivouac found by Neal A. Weber within a large rotted tree stump in British Guiana is the only one which has been described in any detail (Weber, 1941). It is noteworthy that the queen in this colony was physogastric and laid eggs for two days after which her gaster returned to the contracted condition. Weber reported that in addition to eggs he found "very young larvae" and pupae. I have examined about 500 specimens of brood taken by Weber from that colony and have found larvae ranging in age from those at hatching to mature larvae including some within cocoons. In addition, there were pupae which appeared to be of all ages and even some recently emerged callows.

A total of five physogastric and two contracted queens of *coecus* are known according to the summary by Borgmeier (1955: 82-83). These data together with that from the bivouac found by Weber suggest that the queens of *coecus* remain physogastric for a longer period than those of *Eciton* spp. They must lay eggs over a period of at least three weeks in order to produce a nonsynchronous brood such as found by Weber, but it is unlikely that the queens lay eggs continuously. The two contracted queens probably were found between their oviposition periods, but they may have been virgins. Unfortunately, since the dates when these two queens were taken are not known, it is impossible to tell whether these queens were taken at the time of year when sexual broods are produced.

No detailed descriptions of emigrations have been published; however, a few long covered columns mentioned in the literature may have been emigration columns. Brues (1901: 353) stated that *coecus* "moves only by tunneling underground," which is probably true for the most part. However, epigaeic nocturnal emigrations probably take place on rare occasions especially under humid tropical conditions and with the use of tunnels made by the ants.

Labidus coecus perhaps feeds on a greater variety of substances than any other species of Ecitonini. Like other army ants it pri-

marily eats arthropods. However, *coecus* does not seem to prey as extensively on ants as do the other army ants which I have seen. On Barro Colorado Island *coecus* was observed feeding on Amphipoda, Araneida, Scarabaeidae, Cicadidae, Mantidae, Tettigoniidae, numerous moths belonging to a number of families, and several species of small ants. Most of the larger insects were attacked below a wall which had a strong light for attracting male Ecitonini and other insects. The army ants attacked about five to ten times the number of insects which they actually killed at the light. Even when an insect was killed, the ants sometimes abandoned it without doing any visible damage or after removing only part of the appendages. Vibrating these dead insects with a pair of forceps would usually result in a renewed attack on the part of the *coecus*.

In addition to the above insect prey, *coecus* has been reported to eat insect larvae and adults found in and under logs, cow manure and carcasses of dogs, cats, cattle or other animals (Wheeler, 1910: 264; Lindquist, 1942: 851-852). It is problematical whether or not the ants eat any part of the carcasses themselves. Wheeler (1908: 409) reported that *coecus* feeds on carrion, but later (1910: 264) he stated only that the ants were ferreting out larvae in dead bodies. It has been shown conclusively that *coecus* is an important predator on larvae of the screw-worm, *Callitroga hominivorax* (Coquerel) [= *Cochliomyia americana* (Cushing and Patton)], and other Diptera larvae living in the carcasses. In Texas *coecus* was considered to be the most important species of ant responsible for reducing the number of adult flies emerging from carcasses from about 93% to 4%. Not only did the ants kill larvae on carcasses, but *coecus* even attacked larvae in wounds of animals which were "down but not dead." The army ants also killed "scattered larvae dropped to simulate larvae escaping from wounds while the animals were still alive but per cent of adults from these rose to about 20%." On one occasion *coecus* was seen catching adult blowflies on the carcasses (Lindquist, 1942: 850-852).

Labidus coecus apparently eats more plant material such as seeds and cooked rice (Borgmeier, 1955: 93) and nutmeats of various kinds than does any other species of Neotropical army ant. Wheeler (1910: 264) reported that he "attracted and trapped great numbers of workers by burying a few walnut or pecan kernels in the lawns near Austin." Colony E-165 was found on Barro Colorado Island as the ants were carrying off peanuts dropped by some monkeys in their cage. The workers appeared to be able to smell a salted

peanut placed one to three centimeters away from their column and ran up to it. When worker ants came in contact with a nutmeat, they vibrated their antennae more quickly, bit at the nutmeat and tried to pull it toward their bivouac. One half of a peanut kernel was too large for six of the small workers to move it more than a slight amount. Some of these workers ran back along the column, and soon workers with larger heads came and tugged at the peanut. When these were similarly unsuccessful, the biggest workers with huge heads appeared; and these, along with numerous workers of all the smaller sizes, dragged the peanut toward the bivouac. The maximum number of workers seen to pull a half of a peanut kernel was 12. Some feeding was done on the peanut in the course of pulling it around. However, most of the feeding was done underneath a covering of loose dirt piled over, but not actually touching the peanut. Although workers from this colony, E-165, readily attacked the peanuts, ants from three other colonies of *coecus* showed little interest in peanuts placed next to their raid columns.

The entire length of the epigaeic raid column along which these ants carried the nutmeats was about 2.2 meters. The ants came out of a hole in the ground, and the first 20 cm. of trail extending from the hole was covered by a tunnel of dirt like that described above under *praedator*. (Both species of *Labidus* had these tunnels primarily along their trails closest to the holes where the ants disappeared into the ground.) Between 1:30 and 7:30 a. m. this tunnel was extended 50 cm., and it was enlarged in several places. The construction of this tunnel was so rapid that the ants would have been able to completely enclose the entire length of their raid column during the period when it was observed. However, tunnel building was sporadic, and in some cases it was impossible to determine what might have initiated this activity. Twice I saw workers drag a half of a peanut kernel to the tunnel which was too small for both the peanut and the ants pulling it. The ants dropped the peanut and enlarged the tunnel before making a second attempt. After several attempts to get one piece down the tunnel, the ants dropped it and built the tunnel out around the nutmeat.

When *coecus* finds large insect prey which is not readily carried by one or a few ants, it also builds a dirt covering over it. The largest of these dirt domes were about one centimeter in height and five centimeters across with no supporting pillars. These dirt coverings are undoubtedly an important adaptation protecting the ants

from desiccation. Around 7:00 a. m. when the sun started shining on the area of their raid, the workers no longer were seen in the open, but they continued their activity under the dirt coverings. By 8:00 a. m. the ants had withdrawn even from these tunnels and were active only under a brick and in a well-shaded section of the tunnel. The army ants also constructed a wall of dirt around the edges of the brick and repaired this wall after the brick had been lifted. No raiding activity was seen along part of the edge of the brick, but nevertheless, the wall was replaced. Perhaps this species of army ant is highly sensitive to air currents. When the ants withdrew from the more exposed parts of their raid columns, they abandoned a large proportion of the food. It is true that I supplied them with about 15 halves of peanuts and 12 large insects which is probably more than they would find in most places; however, it suggests that *coecus* may frequently abandon a large amount of food which it kills. On two occasions *Pheidole* sp. finished eating the food as soon as the army ants left it.

Five cicadas ranging in size from three to five centimeters, two May beetles about two centimeters long, and two tettigoniids were placed among the ants. These were all promptly killed primarily by biting. *L. coecus* rarely appears to sting its prey and also does not pull the appendages out straight or pull them directly off the prey as do species of *Eciton*. Compared with *E. burchelli*, *coecus* was much quicker at dissecting the large cicadas and scarabaeids. Even the smallest worker can give a person a bite which is easily felt except where skin is quite thick. A single insect about five centimeters long would have at least 200 workers attacking it and covering every surface except some broad smooth hard surfaces such as the elytra of beetles. When a large insect being attacked by numerous ants was quickly picked up, from 50 to at least 100 workers remained in the exact spot where the prey had been. These workers, like guard workers, reared up with their bodies vertical and constantly waved their front and sometimes their middle legs while rapidly vibrating their antennae. The workers remained in this position for at least five minutes. A large amount of raiding activity near by did not cause a decrease of excitement among the workers around the previous location of the prey but lengthened the time they would stay in their erect position to at least 15 minutes.

Since *coecus* is also attracted to vegetable oils, perhaps the attraction to nutmeats can be attributed to the oil in them. In Costa Rica, furthermore, a large number of workers became trapped in lard which they apparently tried to eat (C. W. Palmer, in letter).

Although *coecus* will readily bite people and presumably attacks all vertebrates in the path of its raids, I know of no good evidence that this species actually eats any vertebrate. Weber (1941: 326) reported that *coecus* killed 22 young chickens in British Guiana, but he gave no indication that any parts of the chickens were eaten.

Raids of *Labidus coecus* are somewhat intermediate between swarm raids and column raids. Epigaeic columns are rare, and when present for either a long distance or for more than a few hours, the columns are probably covered by dirt. Bates (1863, v. 2: 365) claims to have followed their tunnels occasionally for a distance of one or two hundred yards. It is most probable that such long tunnels were used for emigrations. In Panama, the typical raid consisted of ants pouring out of from one to over 20 holes in the ground. These ants would form a small swarm on the forest floor and were never seen to go higher than five centimeters on vegetation or on a building. The swarms observed showed little progress in any direction over a period of several hours, possibly because of abundant food in close proximity to the holes. Raid columns were observed between sections of the raid swarm and adjacent to the swarm, but no columns longer than eight meters were seen. The raid swarms often consisted of a number of rather dense masses of workers only ten centimeters wide advancing across the ground and connected by a column less than a meter in length extending to a hole in the ground. A large number of these small masses or swarms connected to branching columns extending to numerous holes would comprise the entire swarm raid. The lack of a distinct direction of progress made these raids of *coecus* appear much more disorganized than those of *praedator*. The *coecus* raid swarms expanded on the surface of the ground, and then all the workers gradually retreated into the ground possibly to again emerge on the surface at some distance away. It would seem unlikely that these retreats indicated the end of a raid when they occurred in the middle of the night. Since *coecus* was rarely seen on Barro Colorado Island, each raiding site was rechecked at least on the following night, and several of the areas were searched several times the same day and following days. In all cases after the ants had disappeared, they did not reappear even though peanuts were put at the sites for bait.

Raids of *Labidus coecus* were rarely seen on Barro Colorado Island probably because of the following four characteristics: the raids are (1) seldom on the surface of the ground, (2) primarily nocturnal, (3) small in area, and (4) short in duration. Seven raids of *coecus* were found between 18 May and 29 July 1956, whereas

none were found between 11 February and 17 May. Since more time was spent searching for colonies during the latter period, these data indicate that *coecus* is more commonly seen during the rainy season.

The earliest observation of a swarm raid of coecus was at 7:45 p. m. The latest records of activity in the morning were two colonies both of which were watched intermittently from 1:00 a. m. until 8:00 a. m. by which time virtually all activity had ceased. These colonies were getting an abundant supply of booty, partly due to my adding suitable prey to the area in attempting to increase the raiding, and as a consequence these raids may have been unusually long. On one occasion *coecus* was observed raiding between midnight and 2:00 a. m., and on a second occasion another colony was raiding between 8:10 and 8:15 p. m. In both cases the ants could not be found when the areas were searched between 4:00 and 4:30 a. m. the same night.

Nomamyrmex esenbecki (Westwood)

Nomamyrmex esenbecki has been found from southern Texas to northern Argentina, a range almost as great as that of *L. coecus*. Borgmeier considers three subspecific names to be valid: *esenbecki s. str.* (Argentina, Paraguay, French Guiana, and Brazil), *crassicornis* (Panama southward to Amazonas and Para in Brazil), and *wilsoni* (from Costa Rica northward). Borgmeier (1955: 147) reported that males of *esenbecki s. str.* were taken at the identical locality as males of *crassicornis* but on dates separated by one month. In a later paper he reported that three specimens of *esenbecki s. str.* were taken at the same locality and date as one specimen of *e. crassicornis* (taken in a different year) (Borgmeier, 1958: 201). More collecting may show that these two "subspecies" may be found within the same colony; or, less probably, they may be valid species. There has not been any doubt that all workers and males from Barro Colorado Island belong to the subspecies *crassicornis*.

No bivouac of *esenbecki* has ever been found in spite of the fact that well over 100 colonies have been observed by various workers. In all cases columns of ants disappeared into holes in the ground, and where digging was attempted no bivouac was found. Bivouacs seem to be moved frequently, for the ants are not found in the same area over long periods of time as has been reported for *Labidus*. The best evidence that *esenbecki* may have an activity cycle similar to *hamatum* is that colony E-164 included a contracted queen, a synchronous brood of worker larvae, and a brood of callow adult

workers on an emigration (discussed below). Schneirla (1957a: 125; pers. com.) reported watching for two to 12 hours or more two emigrations of *esenbecki* on Barro Colorado Island and one on Trinidad in which large broods of callow workers but no other broods were seen. Observations on colony E-164 show that the callows of *esenbecki crassicornis* remain much lighter than the older individuals of the colony for at least six days. Since the largest larvae found in this colony were 11.6 mm. long, 0.1 mm. longer than the maximum length for adults, it is clear that the previous brood of adults is still light-colored when a larval brood is full-grown. A single cocoon containing a white *Nomamyrmex* pupa 3.8 mm. long was found in the emigration of colony E-164. Since this pupa is the size of a minim, one would conclude that it must be a rather retarded member of the brood of callow adults. This discovery is the first proof that the worker larvae of *Noma. esenbecki* spin cocoons, but it is still not known whether the male and queen larvae make cocoons. The broods of *esenbecki* as well as the entire colonies are estimated to be between three and eight times the size of those of *hamatum* judging from the durations of emigrations.

Raids of *Nomamyrmex esenbecki*

Borgmeier (1955: 144) lists ten species of ants attacked by *esenbecki*, including *Cephalotes atratus* L. and *Pheidole* sp. which have been seen to defend successfully their nests from species of *Labidus* and *Eciton* on Barro Colorado Island. Workers of *esenbecki* from the locality seemed timid, could not sting my hands and could scarcely bite the skin between my fingers. Therefore, it seems unlikely that such a weak ant could successfully capture the heavily armoured *Cephalotes atratus* which even *E. burchelli* rarely killed. Several estimates of booty found in raid columns of *esenbecki* on Barro Colorado Island indicate that ants are the main food of this army ant, at least 80 to 90% of the booty being immature ants. Schneirla (1957a: 128) also reported that *Nomamyrmex esenbecki* captures soft-bodied "insect brood" and is "competitive to an appreciable extent" with *Eciton hamatum* for food. The preponderance of larvae and pupae in the raid columns in Panama compared with the records published by Borgmeier of numerous adult ants being carried in columns suggests that the South American *esenbecki s. str.* is a much more aggressive army ant. Also included in the summary by Borgmeier is a report that *esenbecki* was seen to carry off *Eciton dulcius*, but the number of *dulcius* captured and other details were not given. This observation is the only one

known to me of *Nomamyrmex* capturing another species of army ant. On Barro Colorado Island *esenbecki crassicornis* was seen to fight a little with workers of *L. coecus* and *L. praedator,* but no army ant carried off any worker of another species. Only on very rare occasions will one species of Ecitonini carry off workers of another army ant. When *esenbecki* (colony E-164) had a raid column touching that of *coecus* (colony E-165), about ten workers of each species traded bites and vibrated antennae at each other for more than four hours. The same individual ants did not persist in this battle for the entire period, but the number of workers stayed relatively constant. Neither species attacked the other army ant as decisively as it attacked other insects near by, and no workers of either army ant appeared to have been injured.

Luederwaldt (1920, quoted by Borgmeier, 1955: 144) reported that *esenbecki s. str.* attacked termite colonies and bee hives [= Meliponinae?] in addition to ants. In Panama *Nomamyrmex esenbecki crassicornis* also avoided attacking many adult insects such as cicadas and beetles the same species of which were readily attacked and cut apart by other army ants such as *Labidus coecus.*

During 1955 and 1956 I observed 17 raid columns from between 14 and 16 colonies of *esenbecki crassicornis* on Barro Colorado Island. These columns were found primarily during the day including 12:30 and 2:50 p. m. in the dry season. It is clear from the data that *esenbecki* does considerable diurnal raiding, but it cannot be reliably determined whether more raiding is done during the night. Colony E-164 was first found at 1:00 a. m. on 18 May 1956 when it had a raid column extending about 15 meters near the west edge of the laboratory clearing. This column was steady and one to three ants wide with occasional myrmecophiles running along it in both directions. The column disappeared about 10:00 a. m. but in the evening it began again, and gradually shifted to an emigration which will be discussed in detail below.

Most of the raid columns observed were weak ones, only one or two ants wide and extending a few meters on the surface of the ground. The ants ran primarily under leaves and other objects making it difficult to find and follow their columns. The workers were observed to enter almost every crack in the ground which they crossed. In most cases the ants came out of these cracks a few centimeters away, but the ends of all columns entered similar cracks and holes with no further epigaeic columns being found near by. On one occasion a column went up a tree and could no longer be seen when it was at least 15 meters from the ground. This column

was watched from 9:55 to 11:40 a. m. on 12 February 1956, and it probably continued for at least another hour. Larvae and pupae of ants were the booty recorded being carried down the tree. Such raiding high in trees seems unusual for an army ant which otherwise is so markedly subterranean that its bivouacs have never been found, and epigaeic emigrations are rarely seen. Moreover, this raid occurred on a clear day during the dry season when the preceding week had only 0.01 inch of rain. No raid column of any other colony was seen to go even a few meters up a tree.

Where the distal ends of raid columns could be observed, it was clear that *esenbecki* is a column raider with only small groups of workers extending the columns and showing no tendency toward formation of a swarm raid. Compared with *Eciton* spp., *Nomamyrmex* moves across the ground more slowly, perhaps due to its shorter legs. Dirt tunnels covering raid columns were seen only on one day, 29 June 1956, at 8:00 a. m., when a raid column of colony E-199 was followed for about five meters. About three meters of the trail had been covered by tunnels which were scattered along the route in lengths of 20 to 40 cm. Between sections of tunnel the workers ran along open ground which was as exposed as the areas with tunnels. Since some of the tunnels were on branch columns running in different directions, it is unlikely that these tunnels had been used earlier for an emigration. Bates reported that *esenbecki* "always" moved under objects and constructed dirt tunnels or arches if it had to move across an open space (1863, v. 2: 364).

Emigrations of *Nomamyrmex esenbecki*

The major part of one impressive emigration and the probable ends of two others were observed on Barro Colorado Island during 1956. The raid column of colony E-164 had been watched almost constantly from 1:00 to 9:55 a. m.; and although numerous workers and myrmecophiles ran in both directions, all booty was carried toward the old bivouac. The markedly increased traffic about 5:30 a. m. appeared to be the start of an emigration. By 6:30 a. m. the sun was shining brightly on at least three meters of the column, and there was a gradual increase in the amount of ant traffic up to 9:30 a. m. Between 9:30 and 10:00 a. m. the traffic rapidly decreased to nothing. It is possible that the emigration had already begun during this period since part of the colony may not have returned to the old bivouac before the column stopped (due to effects of sunlight?). In the evening of the same day at 6:10 p. m. a raid column two to three ants wide was again bringing in booty along

the identical trail, and myrmecophiles were running in both directions along the column. At 7:20 p. m. the first clear sign that the ants would emigrate was that a few pieces of booty were carried in the opposite direction from all booty seen previously. The majority of myrmecophiles were also running away from the bivouac to which the majority of booty was being carried; however, this had been true during the morning also when no emigration had taken place. During the entire period of observation in the morning not a single callow worker had been seen. After 7:00 p. m. a few callows started to appear, and the number of callows increased to about ten per cent near 9:00 p. m. Although more than 60% of the older workers and all the callows were moving toward the new bivouac, by 9:00 p. m. an occasional piece of booty was still being carried back toward the old bivouac. At the same time guard workers began to stand along the edges of the column. These guards were not all the largest workers, but there appeared to be a slight preponderance of larger workers compared with the distribution of sizes running in the column. A light rain between 9:32 and 9:50 p. m. did not interrupt the emigration but may have slowed the ants slightly. The column broadened to three to five ants wide and remained this width until observations ended at 11:30 p. m. By 9:50 p. m. no more booty was seen going toward the old bivouac. Traffic on the emigration column was so dense and rapid that it was almost impossible to collect myrmecophiles without disturbing at least several workers. Most collecting was abandoned to avoid holding up the emigration or perhaps even stopping it. The number of guards increased, and some workers even ran two to five centimeters out from the column for at least the stretch of three meters of trail visible to me from my observation spot. The latter behavior has never been observed along any portion of an *Eciton* emigration route except at the exact places where a disturbance of the column took place. I had not done any collecting along most of this area and probably could not have caused the increase in excitement shown by the ants. By about 10:10 p. m. each row of guard workers along both sides of the column had a density of at least one worker per centimeter. Some of these guard workers were then standing with their front legs off the ground and with their antennae vibrating rapidly. Within the next ten minutes there was a much more pronounced increase in excitement. The number of guard workers at least doubled, and workers were constantly running on the ground outside the row of guards in a direction

perpendicular to the column for distances of about five centimeters and then running back to join the guards or the emigrating workers. At 10:21 p. m. a pronounced wave of excitement passed along the column indicating that the queen was probably near. At 10:28 p. m. the queen was spotted moving more slowly than the workers and covered with limulodid beetles. The column did not widen when the queen came along, but the workers accompanying the queen appeared to move faster. Except for a slight increase in speed and an increase in excitement shown by the workers near the queen, no retinue could be distinguished. There had been so much excitement shown by the workers during the preceding 20 minutes that the actual arrival of the queen did not stimulate a great increase in excitement as is often the case with queens of *Eciton*.

In addition to the brood of callow adult workers, there was a brood of worker larvae ranging in length from 1.2 to 11.6 mm. A small amount of brood was carried just before the queen passed, and the amount increased slightly until 11:30 p. m. when observations were temporarily ended.

For one-half hour during the remainder of the night it rained a total of 0.27 inch which may have interrupted the column for a few minutes. At 7:00 a. m. the following morning (19 May) the emigration was still in progress. The only differences noted from the previous night at 11:30 p. m. were: (1) the number of guard workers had decreased slightly (but these still lined the route almost continuously on both sides); (2) the rows of guard workers were slightly closer together making a passageway 1.0 to 1.5 cm. wide; (3) the moving column was only one to two ants wide; and (4) the traffic toward the new bivouac consisted of over 95% callows. The guard workers, as during the previous night, were all dark ants contrasting greatly in color with the band of light workers between the rows. In some places the guards straddled the column with their legs, and some guards stood on top of others forming a tunnel of workers. More than 95% of the guard workers at this time were facing in toward the center of the column. The percentage facing inward during the night before had been considerably less, but no record was made. In the morning a branch column one meter in length came out of the ground about one meter from the main column and joined it. Along this column guard workers were present but not so numerous.

Larvae were being carried exclusively by dark workers which also carried an occasional callow. The majority of brood must

have been transported during the night when observations were interrupted. However, thousands of larvae were still carried between 7:00 and 11:00 a. m. Observations were not made continuously during this period while the column was gradually decreasing in strength. By 11:40 a. m. between 10% and 30% of the ants running toward the new bivouac were callows. The proportion of ants returning toward the old bivouac had increased to 30% of the total traffic, and the returning ants were still all dark individuals. Some of these may have been starting to backtrack because the queen had been removed from the emigration column. Guard workers were still scattered along the column every few centimeters, and a few myrmecophiles were running along the column toward the new bivouac.

The emigration was still progressing at 2:30 p. m. on 19 May, but no guard workers were present, and the column was a single ant wide. Dark workers were running in both directions in approximately equal numbers, but callows and myrmecophiles were still seen running only toward the new bivouac. However, between 2:30 and 3:00 p. m. 15 callow and four dark workers were seen being carried by old workers, and in the same period only nine callows were seen running. Earlier the proportion of callows seen being carried was much less. A similar increase in callow and dark workers being carried has been noted at the end of emigrations of *E. burchelli* and other species. By 4:45 p. m. the emigration was considered terminated since only one dark worker was seen every 20 to 30 cm. along the trail. At 7:00 p. m. the trail was visited again, and the backtracking column included callow and dark workers going in both directions. Later in the evening a raid column was seen near by which undoubtedly came from the new bivouac, and the backtracking column apparently continued with little interruption for at least four days.

The majority of traffic on the backtracking column went along the branch trail mentioned earlier. This trail is not the one over which the queen had emigrated indicating that the ants do not stop backtracking at the point where the queen is taken and do not restrict their backtracking to routes over which the queen has passed. Throughout the period of about four days, when backtracking was observed, the ants gradually deviated more and more from the route used on the emigration. On 22 May both dark and callow workers were carrying larval brood in both directions along the backtracking column. The callows were only slightly darker in color than those seen on the emigration on 18 May.

The end of another emigration (colony E-160) was watched from 8:10 to 8:20 a. m. on 14 May 1956. Four workers ran into the hole in the ground between 8:20 and 8:35 a. m., and myrmecophiles continued to run along the trail until 8:55 a. m. A raid column came out of the same hole into which the ants were emigrating throughout the period from 8:10 to 10:00 a. m. The raid column was easily distinguished from the emigration column by the booty being carried toward the hole, by the traffic being approximately equal in both directions, and by the much smaller number of myrmecophiles in the raid column. On 18 July 1956 the end of a probable emigration column was also observed from 11:25 to 11:30 a. m. (colony E-215).

Interrelations Among Individuals of *Nomamyrmex esenbecki*

When workers were released into the dish with queen E-164, the workers ran around the dish and over the queen in an excited manner for about one minute. Then the workers rode on the gaster of the queen or stood with their heads over the queen without licking her. When the queen ran around the dish the workers followed. A total of 14 workers was added to the dish, but within 36 hours eight were dead or so weak that they could no longer keep up with the queen when she walked quickly. Workers rode only on the gaster of the queen, but even active workers had difficulty staying on the gaster when the queen was running. Table 4 summarizes a record kept of the abdominal segments near which the workers held their heads when standing on or next to the queen. The totals are far different from those recorded for a queen of *hamatum*. Although, compared with *hamatum*, many more of the workers seemed to be attracted to the segments behind the first gaster segment, there was no attraction to the genital opening or anus of the queen. Workers were attracted to the lateral and ventrolateral areas of the second, third and fourth gaster segments, but not to these areas of the fifth. Workers were seen to lick the head, thorax, fifth gaster segment, one front leg and an antenna of the queen. Much more cleaning or licking of this queen was observed than for a comparable period of observation of any of the *Eciton* queens. At least twelve limulodids were almost constantly riding on the queen. These beetles licked the queen much more than they licked any of the workers and much more than the workers licked the queen. At no time did the workers attack the beetles on the queen.

Most workers of *esenbecki crassicornis* died in the laboratory

within 24 hours after they were collected. A small number of workers of E-164 kept in a petri dish with their queen, booty from their emigration and water were dead or dying within two days. The queen remained active and not only walked around the dish but attempted to climb the sides several times. The queen never paused to drink or feed at the water-soaked cotton or booty in the dish. However, when a small wad of wet cotton was held up to her mouthparts with forceps, she spread her mandibles and drank some of the water. She also licked a piece of ant pupa which was broken open and held in front of her. Like the workers, the queen vibrated her antennae constantly as she walked, and the recurved distal portions of the flagella touched the floor of the dish. The queen was placed in Bouin's fixative when she was still active on 20 May 1956 at 5:00 p. m. A description of this queen has been published by Borgmeier (1958a).

Flight Dates for Males of *Nomamyrmex esenbecki*

Borgmeier (1955: 150) records a male taken in April 1930 at Balboa, Canal Zone, and one taken in May 1946 at Barro Colorado Island. Additional records for males found at lights on Barro Colorado Island during 1956 are as follows (with the number of males in parentheses): 22 May (1); 5 June, 2:30 to 3:00 a. m. (12, including one which lost wings when taken); 6 June, 5:15 a. m. (8, including 4 which lost wings immediately); 16 June, 4:30 to 5:30 a. m. (1); 17 June, 5:00 to 6:00 a. m. (3). Several of the males were seen flying from the forest to the lights on 5 June and 6 June, and it may be significant that these males were all taken between 2:30 and 6:00 a. m.

Nomamyrmex hartigi (Westwood)

Nomamyrmex hartigi ranges from Paraguay northward to Panama where it is known from both the Atlantic and Pacific sides of the isthmus in the region of the Canal Zone. The species has not yet been found on Barro Colorado Island, but some specimens were sent to me by Wilford J. Hanson who found them in the Canal Zone at Cerro Galera, K-6 road, on 19 January 1959. Of particular interest are his observations that the ants were raiding termites and going up the tunnel made by the termites on the side of a tree. When the tunnel was broken the ants formed bridges and walls in the gaps. Borgmeier (1955: 159) reported that Schwarzmaier observed *hartigi* raiding termites and *Atta* in Goias, Brazil.

Neivamyrmex pilosus (F. Smith)

Neivamyrmex pilosus, which has been been found from Texas and Arizona to northern Argentina, has a wider range than any other species of *Neivamyrmex*; in some localities it is the most abundant species of army ant. On Barro Colorado Island *pilosus* is relatively rare but is the most commonly seen species of the genus. During 1956 we found columns of eight colonies compared with a total of four colonies of three other species of *Neivamyrmex.* Borgmeier (1955: 372-375) has included five subspecies within *pilosus,* but these can be distinguished only on the basis of males. The queen has been found for one subspecies. The subspecies *mexicanus* (F. Smith) has been found from Texas to Panama, including Barro Colorado Island.

Bivouacs of *pilosus* are subterranean or within logs, but no bivouac has been described. Eidmann (1936: 32) reported that the larvae seen in an emigration were all of the same approximate age, and thus he concluded there must be a regular reproductive cycle. We found larvae ranging in size from 2.4 to 4.8 mm. in an emigration column (colony E-227) on Barro Colorado Island. This evidence for synchronous broods and the lack of reports of permanent or semipermanent bivouacs support the hypothesis that *pilosus* may have regular nomadic and statary phases. The two queens which have been found were both contracted and taken in columns (Borgmeier, 1955: 283; Schneirla and Brown, 1950: 325).

Raids of *Neivamyrmex pilosus*

It is clear from observations on Barro Colorado Island, as well as from the literature summarized by Borgmeier (1955: 366-369), that *pilosus* has column raids. The largest, most active raid columns had distal groups of advancing workers forming miniature swarms ten to 40 cm. wide. Most columns had much smaller advancing groups which moved solely in narrow columns. Ants carrying booty along raid columns were seen to disappear into holes in the ground in several places a few meters apart. However, there was no indication that these holes were abandoned and others used during the course of the raid as happens frequently with *Labidus praedator.* There were two characteristics of the raid columns which distinguished them from those of other Ecitonini seen on Barro Colorado Island; (1) at times almost all of the workers were carrying booty, and all the ants were running in the same direc-

tion, and (2) the workers came along the columns in spurts or in groups with gaps between the groups where there were few or no workers for one to several meters. One of these surges of ants changes the column suddenly from a few scattered workers to a tightly massed group two to five ants wide extending for five or more meters. Although fluctuations in traffic are common along columns of all army ants, these changes appeared to be much more distinct with *pilosus*. Nevermann also observed the ants running in the same direction and found that emigrations ended quickly without any stragglers (reported by Reichensperger, 1939c: 300).

On Barro Colorado Island all colonies were found between 14 May and 5 August 1956, indicating that the species does not raid frequently if at all on the surface of the ground during the dry season. Three raids were found between 1:00 and 6:00 a. m., and five were found between 10:00 a. m. and 2:00 p. m. One colony had an active raid on 28 May 1956 between 1:25 and 1:45 p. m. which would be during the siesta period for *Eciton* spp. All booty seen indicates that *pilosus* feeds almost exclusively on species of ants the same size as itself or somewhat smaller, and captures adults, larvae and cocoons. A preference for *Crematogaster* reported by Borgmeier (1955: 367) was further substantiated by booty in several columns. The workers were also seen carrying a small spider, but they were not attracted to peanuts placed beside their columns. This species of *Neivamyrmex* has a more severe sting and bite than many of the larger army ants such as *E. hamatum* and *dulcius*.

Emigrations of *Neivamyrmex pilosus*

On 17 May 1956 a raid column (colony E-163) had been watched between 6:45 and 7:00 a. m. as the raid was ending. The following day at 1:00 a. m. no ants could be found along the route of this column or near by, but by 1:45 a. m. there was a strong raid column. About 4:00 a. m. this raid column shifted to an emigration, judging from the reversal of the direction in which booty was being carried. However, between 6:30 and 7:00 a. m. the emigration abruptly ceased before any brood, myrmecophiles, or the queen had been seen. No column was seen again in this locality even though the area was searched several times during the following night. An emigration column of a second colony was watched from 9:50 to 11:00 a. m. with similar results.

Flight Dates for Males of *Neivamyrmex pilosus*

Males were taken at lights on Barro Colorado Island on the following dates (with the number of males in parentheses): 30 March 1952, about 1:00 a. m. (1); 1 April 1952, 10:00 to 11:59 p. m. (5); 25 March 1955 (1); 28 March 1955 (2); 29 March 1955 (1); 18 April 1956 (1); 19 April 1956, 12:30 to 2:00 a. m. (2); 21 April 1956 (1); 28 April 1956 (7); 3 May 1956, 2:00 a. m. (1), 4:30 to 5:00 a. m. (5); 8 May 1956, 9:30 p. m. (1); 9 May 1956 (1); 10 May 1956, 9:00 p. m. (1); 11 May 1956 (1); 12 May 1956, 5:00 a. m. (1); 16 May 1956, 6:45 a. m. (4); 18 May 1956, 4:00 a. m. (4). The above 40 males were taken between 25 March and 18 May, and Borgmeier list five additional records for males taken within these dates in Panama and Costa Rica. In Mexico and the southern United States the flight dates are later, ranging from 30 May to August (Borgmeier, 1955: 374).

Neivamyrmex gibbatus Borgmeier

Neivamyrmex gibbatus is a fairly common species known from Costa Rica, Panama, and British Guiana. The male is unknown, but a contracted queen was taken by R. Z. Brown from an emigration column on 19 January 1948 at 11:00 p. m. (Schneirla, 1958a: 219). During 1956 I found two colonies raiding at night during the rainy season. The first (colony E-158) was watched from 3:25 to 4:35 a. m. on 3 May, when it had one strong raid column three to five ants broad extending southward from a hole in the ground. In addition, two weaker columns went toward the north and northwest. When the main column was visited again at 5:50 a. m., it had decreased to a column one ant broad, and the other two columns had vanished. This column was followed for about 25 meters on the surface of the ground until it disappeared down two or more holes. Much booty consisting of larval, pupal and adult ants was being carried; and if the column was disturbed, the workers carrying booty would stream in opposite directions along the trail. Other workers rushed out from the trail at the point of disturbance. All workers could give a painful sting without any lasting effect, but their bites were ineffectual except on tender skin.

A second colony (E-241) was found raiding at 9:25 to 9:50 p. m. on 7 August 1956. This raid column was ten ants wide, which is exceptionally wide for a raid column of any species of army ant. In spite of the large numbers of ants along the column, there was no swarm at the distal end of the column. The main column branched,

and the advancing ants stayed in narrow columns or fanned out to form miniature swarms 20 to 30 cm. wide. All booty collected from this raid column consisted of immature and adult ants of several species. On the following day at 7:15 to 7:25 p. m. there was a raid column in the same locality. At the ends of several raid columns when the workers were withdrawing from the area, there were no, or at most only one or two, workers running back in the opposite direction from the retreating ants. The only stragglers seen were two injured workers and two probably myrmecophilous Thysanura.

At one point the raid column of E-241 touched a raid column of *Eciton dulcius crassinode* (colony E-242). The two species avoided each other without fighting, possibly because both columns were a single ant wide and not raiding vigorously.

Neivamyrmex humilis (Borgmeier)

Neivamyrmex humilis previously had been known from a single locality, San José, Costa Rica. It must be a relatively common species there since H. Schmidt found a number of colonies and seven queens. He also found 15 males, nine dark male pupae apparently ready to emerge and some workers in a raid column of *Eciton vagans*. Presumably the *humilis* had been captured by the *vagans*, but no further information was given (Borgmeier, 1948a: 197). The time of year when males of *humilis* are produced is still unknown.

This small orange army ant was found raiding between 11:00 and 11:30 p. m. on 26 July 1956 in the laboratory clearing on Barro Colorado Island. The raid column extended a maximum of six meters from a hole in the ground and had at least four branches. One branch went about 30 cm. up the side of the laboratory where the army ants were raiding an ant colony. A staphylinid larva was taken as it was running along in the midst of the army ants. No other myrmecophiles were seen, but a diapriid was later found among the aspirated ants. The ants were carrying one small spider, one immature homopteran, some adult ants, and numerous larvae and pupae of ants.

Bright white light did not disturb the raid column as much as it does columns of other species of army ants, but aspirating ants caused workers along the column to rear up in the typical position of army ants when highly excited. Similar behavior resulted when a small, partially crushed cricket (Gryllidae) was dropped on the

raid column. The cricket was still moving, but the ants would not attack it. The workers made a ring around the cricket with all the ants facing it. Occasionally one worker would rush toward the cricket until the ant's antennae touched the gryllid, and then the ant would rapidly run backwards. The raid column made a detour around the cricket, and no worker attacked it. The *humilis* workers seemed unable to sting my hands, and their bite was weak.

Neivamyrmex postcarinatus Borgmeier

Neivamyrmex postcarinatus is known only from Barro Colorado Island. Previous reports are limited to the type series collected by Schneirla on four dates: 21 February 1946, 8 March 1946, 18 March 1946, and 16 January 1948. On 1 February 1955 I watched one raid column from 9:45 to 10:00 p. m. It is of interest that all five records fall between 16 January and 18 March during the beginning and middle of the dry season. The raid column which I observed followed the buttress root of a huge tree for at least eight meters, and this same route had been used by both *Eciton burchelli* and *E. hamatum* colonies within the preceding two days.

Neivamyrmex opacithorax (Emery)

Neivamyrmex opacithorax has a range approximately equivalent to that of *Neiv. nigrescens* in the United States, and in addition the former species extends southward to Costa Rica. Both species are found throughout most of the southern states from California to North Carolina and extend farther north in the plains states, Kansas, Nebraska, and Iowa (M. R. Smith, 1942: 558; Borgmeier, 1955: 504).

There are a number of seemingly contradictory statements in the literature regarding the relative abundance of these two species. Cole (1953b: 84) reported that *opacithorax* was much more common in New Mexico than *nigrescens*. In the Gulf States, M. R. Smith (1942: 560) reported that *opacithorax* is "never so abundant as" *nigrescens*. Schneirla (1958a: 221) reported that in Arizona *opacithorax* is "perhaps as common" as *nigrescens*, but he also stated, "more than 12 colonies of *Neiv. nigrescens* and 6 colonies of *opacithorax* were found . . ." (p. 241). Part of the above discrepancies may be explained by the report that *nigrescens* is more abundant in the southeastern United States compared with farther west (Creighton, 1950: 65). Perhaps of more importance are the precise habitats of the two species. In Kansas, *opacithorax* has

been found in open fields, and in park-like areas within cities. *Neiv. nigrescens*, on the other hand, has not been found in these areas but was found within more moist wooded areas. Although this conclusion has been based on a total of only about 15 colonies of the two species found in Kansas, it suggests that *opacithorax* may be restricted to drier areas throughout the country.

Raids of *Neivamyrmex opacithorax*

Neivamyrmex opacithorax appears to feed almost exclusively on ants and carabid beetles. The capturing of larval and adult Carabidae seems to be a common occurrence since three colonies of *opacithorax* in Kansas had killed numerous specimens, and Wheeler and Long (1901: 163) reported that *opacithorax* in Texas had captured "a considerable number of small carabid beetles." Ants probably are more frequently killed in all localities, and ant larvae taken from raid columns showed no movement, probably indicating that they are killed by stings of the army ants at the time of capture. Workers from three colonies showed little attraction toward pecans, English walnuts or roasted peanuts, but two workers at one time chewed on a piece of walnut for about five seconds.

Raids of *opacithorax* primarily occur in the evening, night and early morning. On cloudy days raids may be extended throughout the day, but the ants rarely raid in sunlight. In all cases the raids seen were column raids with no tendency toward swarm raids. On several but not all raid columns each incoming ant carried a piece of booty. It appears that *opacithorax* may be more efficient than the common species of *Eciton* in that fewer *opacithorax* workers return without prey. It is uncommon to see two or more workers of *opacithorax* carrying a single piece of booty, whereas such tandem carriers are frequent among *Eciton* spp. The column raids of *opacithorax* look inefficient at capturing prey since the ants do not run up low vegetation including even short blades of grass. Numerous insects retreat a few centimeters up on objects and completely escape the ants. The raid columns often show greater fluctuations in traffic than those of most army ants observed, but the fluctuations are not as great as those seen along raid columns of *Neiv. pilosus*.

Some additional information on the raiding of this species is given by Schneirla (1958a).

Emigrations of *Neivamyrmex opacithorax*

Three emigrations of *opacithorax* have been seen in Lawrence, Kansas. The first one found occurred on 3 June 1958 starting prob-

ably about 10:00 p. m. When colony E-263 was first visited at 10:25 p. m. that night, there were no raid columns, and a steady emigration column extended from one hole in the ground to a second hole under a dense bush 50 cm. away. The exact location of the subterranean bivouac(s) is unknown, but since 26 May the ants had raided daily coming out of one or more of five holes within a radius of 16 cm. If one considers 26 May as the first statary day, the ants were emigrating on the ninth statary day or approximately the middle of the statary phase. From 10:25 until 11:10 p. m. the emigration column increased in width slightly until it was between three and five ants wide. No callows were seen in the column, and the brood being carried was in the egg stage. By 11:35 p. m. guard workers had positioned themselves along the column. Some of these became quite excited partly due to my collecting. In addition, a lycosid spider walked across the column, and a sowbug and a caterpillar started to walk across and retreated. The caterpillar was severely attacked; however, the other arthropods were not injured. The excited guard workers sometimes climbed as high as two centimeters up on vegetation, and sometimes ran about six centimeters out from the emigration column. At six minutes past midnight the physogastric queen came walking along the column. The column was highly aroused by that time, and there was no discernible wave of excitement due to the advance of the queen. It is possible that the queen had some difficulty getting through the hole in the ground which was just large enough for her to pass. A solid row of guard workers was along 50 cm. of the epigaeic route, but these guard workers were not arranged in a compact wall or tunnel as had been observed with *L. praedator* and other army ants. The queen had about six workers on her in the emigration column, but these were riding and in no way helping her progress along the column. In spite of appearing to be in a maximally physogastric condition, the queen had no obvious difficulty running along the column. The workers of *opacithorax*, like those of other species of army ants, can run appreciably faster than the queen on a level surface. Most of the egg brood was carried before the queen was seen, but additional brood was carried up until about 12:28 a. m. By this time the number of guard workers had markedly decreased in number, but the width of the column remained approximately the same. By 12:34 a. m. all the guard workers had left, and occasionally a packet of eggs was carried by. Before the queen emigrated, one could see more than 25 packets of eggs along a stretch of column 30 cm. long, but by 12:34 a. m. a maximum of one packet

per 30 cm. could be found. Between 12:40 and 12:51 a. m. the column got abruptly thinner, more ants seemed to hesitate and go back along the column a few centimeters, and the first two workers were seen being carried. Several ants were seen to walk more or less sideways, hesitating and picking up dirt and pieces of wood. These workers appeared to be a clean-up squad checking to see whether anything had been left behind. The behavior, which is not seen along the emigration column when it is thronged with actively moving ants, probably is responsible for the carrying of workers and guests more at the end of emigrations rather than during the beginning and middle periods. At 12:54 a. m. the last ants had passed. The end of this emigration made slow progress since the ants ran back along the column and also constantly ran five to ten centimeters laterally from the trail. The caterpillar which had been attacked about 11:40 p. m. was gradually abandoned during the last half hour of the emigration. It struggled constantly while the ants were attacking it and was unable to crawl when abandoned. Observations continued along the trail until 1:31 a. m.; and although no further ants passed, a few phorids and staphylinids were seen.

In addition to the large number of eggs seen being carried on the emigration, the queen from the above colony laid about 9,500 eggs after she was taken. As far as could be determined she did not eat during this period. (More details of the oviposition are given below in the section Oviposition and Queens of *Neivamyrmex opacithorax.*) The exact location of neither bivouac is known; but since the epigaeic emigration column was just 50 cm. long, it is highly probable that this was not a normal emigration. Similar short "emigrations" or bivouac shifts of *E. hamatum* and *burchelli* have been seen during the statary phase. However, the bivouacs of these two tropical species had been disturbed, and the bivouac sites in some cases had been completely destroyed. There was no known disturbance of the bivouac of this colony of *opacithorax.* The holes used by the ants were at the edge of a driveway, and it is possible that the bivouac was under the driveway and in too hot and dry a location for the ants. One colony of *Neiv. nigrescens* emigrated during the statary phase when the queen was nearly maximally contracted, and this emigration was thought to be due to disturbance by a colony of *Pheidole* (Schneirla, 1958: 231-232; pers. com.)

Not a single callow worker, pupa, or larva was seen in the emigration. Although Schneirla (1958a) has given good evidence to support the hypothesis that *Neiv. nigrescens* has a nomadic-statary

cycle homologous to *E. hamatum*, there is no comparable evidence for *Neiv. opacithorax*. This emigration of colony E-263 was undoubtedly atypical since it occurred in the middle of the oviposition period. At that time one would expect a brood of pupae to be present, and perhaps the absence of this older brood was partially responsible for the unusual emigration. (It is unlikely that an entire pupal brood would have been carried by a subterranean route or remained in a subterranean bivouac while the rest of the colony emigrated on the surface.) It is highly improbable that the egg brood found during the emigration on 3 June 1958 was the first brood of the year. *Neiv. opacithorax* has raids on the surface of the ground and can be found in clusters under stones in Lawrence, Kansas, at least as early as 10 April. Broods probably are not produced during the winter, and it is not known when the first eggs are laid in the spring.

On the evening of 4 June about 18 hours after the queen of colony E-263 was taken there was no backtracking column at 6:20 p. m.; however, at 10:15 p. m. a column was going toward the old bivouac site but into a hole about 18 cm. closer to the new bivouac than the exit hole used on the emigration. Thus, the ants were not backtracking along the trail actually used on the emigration but were using a different route of an earlier raid column. A few workers occasionally stuck their heads out of the exit hole used on the emigration, but no workers formed a connecting column on the surface of the ground. Two workers which had been kept in the laboratory with the queen were placed along the backtracking column. There was an immediate wave of excitement followed by an increase in the number of workers along the column. On 5 June a backtracking column was still present, and no further observations were made.

Another emigration (colony E-264) was watched on 6 July 1959 on the campus of the University of Kansas. A raid column had been seen crossing a sidewalk next to Snow Hall during the day at 11:30 a. m. and 12:40 p. m. At these times the ants were going out on the column at a rate of about 50 ants in one minute and six seconds. Less than ten percent of the number of ants going out were returning. By 7:15 p. m. the column had increased to 50 ants going out in ten to 20 seconds with less than five ants going toward the bivouac in the same interval. By 8:45 p. m. traffic was more steady at about 50 ants going out and nearly 12 going in during 12 seconds. Booty

was first seen being carried out at 8:53 p. m., and by 8:56 p. m. larval brood was carried. At this time approximately two percent of the ants carried either booty or brood. However, at 9:02 p. m. the amount of brood increased markedly until about 50% of the workers were carrying brood, and the traffic had increased to its maximum of about 50 ants going out in five seconds. At 11:22 p. m. the ants became more excited, workers ran one to five centimeters away from the column along both sides, and many more workers ran back toward the old bivouac. The queen was taken at 11:41 p. m. Up until 1:35 a. m. on 7 July when observations were ended, the number of ants going toward the new bivouac remained at the maximal rate, and workers went back toward the old bivouac at about 25% of the outward rate. Many callows and a few minor worker pupae were seen in the emigration. Only dark workers were seen returning toward the old bivouac and carrying other workers.

A strong backtracking column was found along the emigration trail between 10:00 a. m. and 1:00 p. m. on 7 July. The column consisted solely of dark workers running in both directions in approximately equal numbers. At 8:00 and 9:00 p. m. the traffic on the backtracking column was the same or slightly stronger. At 7:45 a. m. the following morning the traffic on the column had decreased from its previous strength at night, and the first callow was seen in the column. The column continued throughout the day, and the first brood or booty was seen being carried toward the old bivouac (of 6 July) at 7:00 p. m. The backtracking column persisted until 10 July when it was noticeably weaker at 10:00 a. m. compared to previous days at that time. On 10 July at 6:00 p. m. and the entire following day there were no longer any ants along the trail.

A third emigration (colony E-266) was watched almost continuously from 9:00 p. m. to 3:20 a. m. on 19 to 20 August 1959. Throughout this period numerous callows were seen, and booty and a brood of worker larvae about three-fourths grown were being carried. The queen was not seen, and neither guard workers nor greatly excited running workers were seen, indicating that she probably had not emigrated before 3:20 a. m. On 20 August at 7:30 p. m. there was a weak column of about one ant per ten centimeters (including the approximately equal traffic in both directions). This column had disappeared by the following morning, and it is impossible to determine whether it was a backtracking column (pos-

sibly followed by a continuation of the emigration) or a raid column. Similar columns along previous emigration routes have also been reported for *nigrescens* (Schneirla, 1958a), but such columns are not found or are rare among *Eciton* spp.

Bivouacs of *Neivamyrmex opacithorax*

All bivouacs of *opacithorax* which have been located were subterranean, and their exact positions and sizes are unknown. On five occasions in the vicinity of Lawrence, Kansas, clusters of *opacithorax* have been found under small stones. Each of these clusters was considered to be less than five per cent of the total colony. Similar "bivouacs" under stones mentioned by Schneirla (1958a) probably were not entire colonies. Brood was never found in any of the clusters in Kansas except for the adult males in colony E-267 discussed below. However, *opacithorax* like *nigrescens* probably brings at least part of its brood up from more subterranean bivouacs to areas under stones on the surface of the ground. These stones were all exposed to bright sunlight during the day, and an unusually high number of staphylinid beetles or mounds of loose dirt indicated that the ants had been much more numerous under each stone than they were at the time they were found.

Oviposition and Queens of *Neivamyrmex opacithorax*

The queen from colony E-263 in the laboratory laid 9,500 eggs within 42 hours of the time when she was taken from an emigration column. This rate of oviposition is 226 per hour or 3.8 per minute. Judging from the few colonies which I have seen, the colonies and broods of *opacithorax* and *nigrescens* are essentially the same size. At the above oviposition rate it would take the queen almost seven days to lay a brood of 37,000 eggs. A brood of that size was considered to be average for *Neiv. nigrescens* (Schneirla, 1958a: 242-243). However, it is known from observations on physogastric *Eciton* queens that when these queens are brought into the laboratory, they cease laying sooner than if left with their colonies. In addition, *Eciton* and *Neivamyrmex* queens become noticeably weak and often die within a few days in the laboratory. As a consequence the oviposition rate in a normal bivouac may be considerably higher. Records for the first 19 hours indicate that queen E-263 laid at a rate close to 300 per hour which is probably closer to the rate in a bivouac. At this rate she could have laid a brood of 36,000 eggs in five days.

Actual egg laying occurred in irregular spurts with sometimes more than five minutes between two groups of eggs. The eggs most frequently were laid in groups of two to eight eggs stuck together at their tips. Five or six eggs usually were laid in 30 seconds. The eggs appeared moist when laid and readily stuck together in packets without licking or handling by the workers. The queen often rested partially on her side when ovipositing and frequently walked around the dish scattering eggs wherever she went. The workers gathered up most of the eggs and placed them in piles. Several workers ate some eggs while turning their abdomens under as if they were stinging the eggs at the same time. It is not known whether the workers also eat eggs or other brood in a bivouac, but it is a well-known fact that other Ecitonini eat their brood of all ages more readily in the laboratory than under field conditions.

The queen was kept alive until 6:00 p. m. on 5 June 1958 when she was placed in Bouin's fixative. No eggs had been laid during the preceding hour, and only a few were laid in the last three hours before preserving the queen. As far as we could determine the queen did not eat nor drink anything while she was in the laboratory. The queen from colony D-175 taken by Howell V. Daly from a cluster under a stone also was never seen to feed, but the workers with her readily drank water and fed on a partially crushed housefly. This queen was observed to clean her own antennae with her front legs, but no queen of *Neivamyrmex, Nomamyrmex* nor *Eciton* was observed to clean any part of her body. All queens of Ecitonini usually ran around with their mandibles spread, but they would never bite anything even if an object was placed between the mandibles.

Sexual Broods of *Neivamyrmex opacithorax*

Colony E-267 was found about 2:00 p. m. on 21 October 1959 by people who complained that their home was being invaded by insects coming up between floor boards. Investigation on the following day at 10:00 a. m. showed that the colony had a brood of alate males which were entering the house along with some workers, and additional males were at the edges of the foundation on opposite sides of the house. Workers were more numerous along the inside edges of the foundation where small clusters of up to 200 workers were scattered for more than a meter along the rough field stone foundation. No brood other than the adult males could

be found, and the largest part of the colony (or colonies) must have been under the foundation. Most of the males had a number of workers clinging to them. The two groups of ants were about six meters apart with no ants seen between the opposite sides of the house externally or in the crawl space under the house. These two groups may have been daughter colonies following a colony division.

A total of 52 males was taken and 27 of these were kept alive in a laboratory nest. When placed in this nest at 1:00 p. m. on 22 October, three of these 27 males ran around the nest, tried to fly and were attracted toward a microscope light. Several males clustered with workers on a petri dish filled with moist cotton. Most of the males clearly moved away from the light and slowly walked until they reached the darker corners of the nest. These latter males neither fanned their wings nor flew when dropped. Most of the males had died by the morning of 24 October. The workers pulled

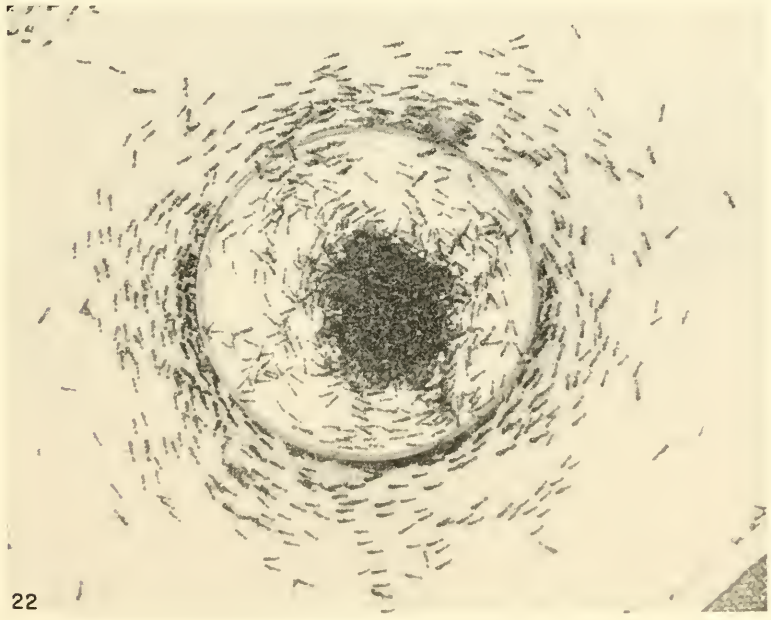


Figure 22.—Workers of *Neivamyrmex opacithorax* running clockwise in circular column around an uncovered petri dish 65 mm. in diameter. Moist blotter paper is in center of dish, and about two thirds of ants are clustered on top of it. No food nor brood is present. Dead ants are scattered around edges of nest (edges of nest at upper left and lower right corners). Column lasted for at least six hours but broke up when dish was removed from center.

the dead males around the laboratory nest a little but did not eat any part of the males nor do any damage to them.

A circular column was found on 25 October at 2:00 p. m. after the males had all died. This column, shown in figure 22, continued for over six hours without any interruption even though the cover of the nest was removed and lights were turned on and off repeatedly.

Published records for males of *opacithorax* indicate that this species has males in September and October throughout the northern part of its range (M. R. Smith, 1942: 558; Borgmeier, 1955: 504). The earliest and latest known collection dates for males of *opacithorax* in Lawrence, Kansas, are "September" and 22 October based on specimens in my collection taken during 1945, 1956, 1959 and 1960. In Florida males have been taken on 10 November 1911 (M. R. Smith, *l. c.*), 9 December 1948 (Borgmeier, *l. c.*); and I found one alate male on 9 February 1956 at 2:00 p. m. along the tide line at Crandon Beach Park, Miami. The latter male was soaked but still alive and probably had been washed up on the beach after falling into the water a few feet offshore. Records from Georgia to Arizona fall between August and November, and one record for Costa Rica is for April (M. R. Smith; Borgmeier, *l. c.*).

Neivamyrmex nigrescens (Cresson)

Neivamyrmex nigrescens has been found from the southern United States to Guerrero, Mexico. As discussed above under *Neiv. opacithorax*, the distribution of *nigriscens* may be primarily in the more moist and wooded areas of the region. The fact that about half as many colonies of *nigrescens* as *opacithorax* have been found in the vicinity of Lawrence, Kansas, is attributed to *nigrescens* being absent or more rare in clearings or within the city. Males of *nigrescens* have been found during the same period as those of *opacithorax* in the United States. However, I have never found any male *nigrescens* in Kansas, and their much greater scarcity probably indicates that colonies of *nigrescens* are less abundant than those of *opacithorax*. Unlike males of the epigaeic species of *Eciton* which fly from emigration columns, the males of *nigrescens* were observed flying from a nest near Austin, Texas (Wheeler, 1910: 263).

Raids of *Neivamyrmex nigrescens*

Neiv. nigrescens has column raids similar to those of *opacithorax*, but it appears to feed primarily on ants and less frequently captures beetles. The following foods were put in a laboratory nest containing about 1,000 workers of *nigrescens:* peanuts, cashew, hazel, English walnut, and black walnut nutmeats, raisins, dried coconut, sugar syrup (sucrose), peanut oil, margarine, butter, bacon grease and ground beef. As far as could be determined, not a single ant ate any of these substances. During the same period the workers were seen to drink water and eat one collembolan and some of their pupal brood. In spite of the large number of pupae which remained alive in the nest, most of the workers died within seven days, and all were dead within 11 days. Since *Eciton hamatum* and *burchelli* readily eat their brood, one would expect that *nigrescens* would have eaten a much larger proportion of the pupae. For further details on the raids of *nigrescens* one should consult the paper by Schneirla (1958a) which is the most thorough study made on the raiding of any species of *Neivamyrmex*.

Emigrations of *Neivamyrmex nigrescens*

The most extensive observations on emigrations of *Neivamyrmex* have been made by Schneirla (1958a) who studied over 60 emigrations of *nigrescens* in Arizona. The general pattern of the emigrations appears to be comparable to that of *E. hamatum* except that the queen "usually makes her journey at some time after the emigration is roughly one-third completed" (Schneirla, 1958a: 245). This statement suggests that the queen leaves the old bivouac much earlier than those of *Eciton,* and perhaps this is correlated with a high position of the queen in the subterranean bivouacs where she is close to the surface of the ground. In addition, emigrations frequently may be started on one night and continued on the following night.

Unlike the typical nomadic phases of *Eciton hamatum* in which colonies emigrate nightly with rare exceptions, it is common for a colony of *nigrescens* not to emigrate on one or several nights during the nomadic phase. A comparison of figures 7 and 23 based on data published by Schneirla will readily indicate the greater number of nights throughout the nomadic phase when colonies of *nigrescens* did not move. These data are not sufficient to show any clear pattern. However, as pointed out by Schneirla (1958a: 250),

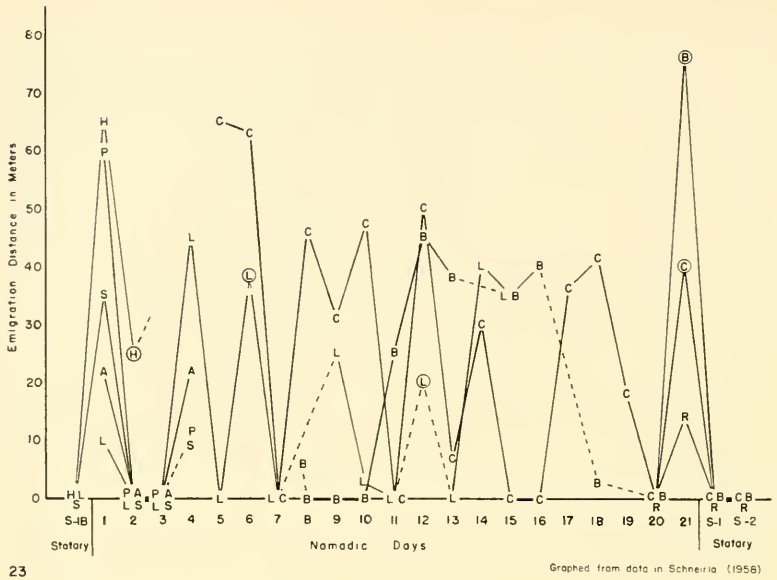


FIGURE 23.—Graph of emigration distances for eight colonies of *Neivamyrmex nigrescens* in Arizona. Data published by Schneirla (1958). Colonies indicated by following symbols: A = Laboratory-A, B = Bridge, C = Creek, H = Skunk Hollow, L = Laboratory-B, P = Pugsley, R = Rock, S = Stone. Circled letters indicate colony completed its emigation of that distance on following night. Dashed lines indicate distance was not known or not published. Exact day in nomadic phase not known in most cases, but estimated from most complete records.

there is a tendency to omit an emigration on the day following the first emigration of the nomadic phase. These data indicate that there is no clear increase in the distance that a colony emigrates during the course of the nomadic phase. One might expect that a colony would have larger raids and would emigrate a greater distance near the end of the nomadic phase, based on the hypothesis of Schneirla that the stimulation of the workers by the larvae increases as the larvae increase in age. Not only is there no clear increase in the distance, but there are three records for colonies which did not emigrate at all on the day preceding the last nomadic day. Although Schneirla seems to imply that the first nomadic emigration is especially "vigorous," figure 23 indicates that the colonies do not necessarily emigrate a greater distance on this emigration than on any of the others. The size and vigor of raid and emigration columns can be expressed in many ways such as the

width of columns or speed of workers, but these other values are more difficult to determine than the length of columns. One cannot conclude that because vigor in raiding and emigrating is not expressed in the length of the columns it will not be expressed by some other variable.

Bivouacs of *Neivamyrmex nigrescens*

All bivouacs of *Neiv. nigrescens* are subterranean, and although typical nests probably extend at least one meter below the surface, two bivouacs found near Lawrence, Kansas, were largely or completely within the upper 30 cm. of soil. Colony E-101 was first found by Dr. Henry S. Fitch at the University of Kansas Natural History Reservation on 28 June 1955 at 9:00 a. m. At that time a mass of workers and brood 15 to 20 cm. in diameter was found under a stone. On the following day at 2:00 p. m. approximately one-tenth as many workers and a little brood were found under the same stone. When the ants were visited again at 9:30 a. m. the subsequent day (30 June), the mass was about 13 by 18 cm. in size. The stone was in bright sunlight most of the day in an area of scattered trees and shrubs next to a more dense woodland. These meager data suggest that the ants bring their larvae near the surface during the afternoon and evening and carry them deeper in the middle of the day if the rock becomes too hot. The brood consisted of worker larvae which were starting to pupate, but since *Neivamyrmex* spp. do not spin cocoons, the shift in larvae was not identical to the movement to spinning areas found in *Eciton* colonies during this period. Schneirla (1958a: 250) concluded that the "statary condition did not ensue in the colonies until the naked brood entered the early pupal stage." However, colony E-101 clearly became statary before any, or at most less than one fourth, of the larvae had transformed to pupae. Thus Schneirla's hypothesis (that the nomadic phase is terminated largely because of the cessation of stimulation by the larvae) is substantiated better by this case than by his records from Arizona. (Perhaps Schneirla's use of "early pupal stage" is equivalent to the prepupal stage.)

Colony E-101 had done considerable digging to enlarge the chamber under the stone and had piled up a mass of loose dirt about three by eight centimeters along one edge of the stone. The stone was relatively flat, approximately 25 by 40 cm., and a small colony of *Crematogaster* was under the opposite side separated from the

nigrescens by two to three centimeters of dirt. When the stone was lifted, there was some mixing of the two species. The *Crematogaster* workers quickly attacked six *nigrescens* and immobilized them by pulling their legs in opposite directions. The army ants were not as successful and did not capture nor noticeably injure any of the *Crematogaster*.

On 30 June 1955 between 9:30 and 10:30 a. m. Dr. Wallace E. LaBerge and I dug out a large part of the bivouac. Even when the ants were numerous and excited, we could not detect any odor from them. However, when a worker of *nigrescens* is crushed between one's fingers, there is a strong acid odor similar to formic and glacial acetic acid. More than 20 chloropid flies, *Madiza cinerea* (Lw.) [det. C. W. Sabrosky], were apparently attracted to the ants or moist dirt, and these flies both flew above the bivouac and ran on the dirt among the ants.

The mass of workers and the brood of larvae, prepupae and a few pupae together occupied about 250 ml. when alive. At least six tunnels extended downward from the area under the stone, and small groups of ten to 75 pupae were scattered in cracks and small chambers. At a depth of 17 to 20 cm. the queen was found, but there was no large mass of workers nor were the workers more excited near her. However, there appeared to be a slightly higher proportion of larger workers near the queen than elsewhere in the bivouac. The queen was at least partially physogastric with a total length of 14.5 mm. when measured alive. This measurement may not be accurate because the queen was somewhat crushed while we were digging. No strong columns nor clusters of ants could be seen extending below about 20 cm., and no further digging was done. Because only about 2,700 larvae, prepupae and pupae were collected (about half the brood seen), probably a large part of the colony was underground in areas peripheral to the small hole which contained the queen.

When the bivouac was partially dug out, the brood was estimated to be at least three-fourths larvae and prepupae and one-fourth pupae.[1] The larvae were rapidly transforming to pupae, and by

1. Schneirla (1957a: 126; 1958a: 218) in referring to my observations on colony E-101 stated that a "small sample of mature larvae and a large sample of pupae nearing eclosion" were taken, and the ants "emigrated a few days after maturing worker pupae had been found in the nest." It is not known when that colony emigrated from the site. However, when the ants were *first* found, the larvae were full-grown and transforming to pupae, and some of these pupae became adults 12 days later in the laboratory. The colony did not emigrate for four days at the beginning of the pupal period, and no subsequent field observations were made to determine when the colony finally did emigrate. Since the queen had been killed and a large part of the brood had been taken, a normal transition from a statary to a nomadic phase would have been unlikely.

the following morning between one half and two thirds of the brood had pupated. By 9:00 p. m. that night over 90% had pupated. Judging from these observations, the entire period of transformation from larvae to pupae takes about four days and probably at least three-fourths of a brood transforms within two days.

In spite of the disturbance of the bivouac, colony E-101 had not left the site by 2 July when an additional layer of dirt and stones five to 15 cm. deep was excavated. Less than 100 pupae were found along with several hundred workers. According to the observations by Schneirla (1958a: 249) in Arizona, *nigrescens* has a statary phase of about 18 days with one brood of pupae, and a second new brood of eggs is laid during that phase. Callow workers of colony E-101 first started emerging on the morning of 10 July which would be the 13th statary day if 28 June is assumed to be the first statary day. However, laboratory temperatures were somewhat above 30° C. during much of this period, and it is quite likely that the length of the pupal period may have been shortened slightly by the temperature. Even though a few callows had emerged, probably several more days would have been required for emergence of at least three fourths of the brood. Since part of the brood appeared to be dying and no workers remained active, the entire brood was preserved. Schneirla (1958a: 233) has reported that a "minority" of the pupal or callow brood was carried on a first nomadic emigration of this species.

A second bivouac (colony E-261) was found on 4 May 1957 a short distance from the bivouac site of colony E-101. This second colony was bivouacked under a stone about 120 by 50 cm. in area with an undetermined number of ants in the soil beneath it. Over 10,000 workers were collected, but no brood nor queen could be found.

Interrelations Among Individuals of *Neivamyrmex nigrescens*

Queen E-101 was unable to walk, but her legs moved slightly, and her gaster pulsed for more than five hours. Her gaster was split along the left side and a homogeneous white mass (fat body?) and fluids oozed out. Examination with a magnification of 40 to 80x showed no sign of eggs in this mass or at the tip of her abdomen. Workers were attracted to the queen but did not lick any of the fluids oozing from her gaster. The workers primarily licked the

knob or ridge on the alinotum and the first and second gaster segments.

The workers of colony E-101 in the laboratory nest gathered most of the larvae, prepupae and pupae scattered in the dirt but ignored many others. The brood was primarily put in three piles on the surface of the soil, and as far as could be determined none was carried into the soil even though the ants made extensive passageways throughout it. The pupae were grasped primarily by their gasters held ventral side up with the mandibles of the adult hooked around the hind tarsi which always were close to the gasters of the pupae. On a number of occasions a worker was seen to turn a pupa completely around end to end and side to side until the adult could grasp the pupa in this preferred position. Much less frequently the workers held the pupae by their heads or gasters with their dorsal sides up.

None of the prepupae nor pupae showed any movement regardless of how much they were handled by the workers or by forceps. When the callow workers started emerging, all the old adult workers which had been collected could scarcely walk or had died. The callows could partially emerge without any assistance, but they walked around encumbered by large pieces of the pupal covering which they could not strip from their bodies. All the callows appeared weak and could hardly walk probably due to the combined effects of hunger and the attached pupal skin.

Cheliomyrmex Mayr

Cheliomyrmex, the fifth genus of Neotropical army ants, includes five extremely rare species placed in the tribe Cheliomyrmicini. The genus ranges from Mexico to Brazil, but too few specimens have been collected to give a clear picture of the range of any species. The first specimen from Panama is a male of *megalonyx* Wheeler taken at Cerro Campana on 21 October 1959 by Wilford J. Hanson. I determined this male by comparison with the type of *audax* Santschi taken in Ecuador and specimens of *megalonyx* taken at Kartabo, British Guiana, and now in the Santschi collection at Basel. (The single specimen of *audax* which was examined is considered to be the type although there is no type label or collector's name with it.) However, the Panamanian specimen agrees more closely with Borgmeier's (1955) redescription of *audax* than with that for *megalonyx*.

What little is known about the biology of *Cheliomyrmex* is based on the observations by Wheeler (1921:319-322) on one colony of *megalonyx* found raiding and emigrating at Kartabo. This species of *Cheliomyrmex*, like *Labidus praedator*, makes tunnels on the surface of open ground and has numerous guard workers when it emigrates. Only larval brood was being carried in the emigration column, suggesting that the broods are synchronous. The pupa and queen are still unknown; in fact, no reproductive of any instar has been found in a colony.

SUMMARY AND CONCLUSIONS

Probably the most important conclusion from this study is that nearly all the additional observations on the behavior of army ants support the conclusions indicated by Schneirla (1933, *et seq.*). Most publications on the behavior of Neotropical army ants are restricted to *Eciton hamatum* and *burchelli*. The observations reported in this paper, although much more limited than those of Schneirla, include a wider range of species and some aspects of the behavior of the ants not mentioned by him. Schneirla and other authors have often discussed the behavior of *E. burchelli* and *hamatum* as the behavior of "*Eciton*." Such a generalization can apply to many of the basic features of behavior such as periodic emigrations and large raids for arthropod prey. However, for many details of behavior such a generalization can be misleading because there are indications that these two species may be the most highly specialized or atypical of the approximately 12 species of *Eciton s. str.* Compared with other species of *Eciton*, *hamatum* and *burchelli* more frequently have epigaeic bivouacs and raiding columns, a more consistent diel rhythm of raiding and emigrating, more reliable backtracking, and more precise structure of their bivouacs.

Raids: Most species of army ants obtain food by means of column raids with small groups of ants entering new territory at the ends of columns advancing from the bivouac. *E. burchelli* and *Labidus praedator* have, instead, swarm raids, *i. e.*, large masses of ants advancing at the fronts of fan-shaped areas of anastomosing columns. The base column of *praedator* is usually subterranean near the bivouac and as the swarm front advances, the subterranean columns are extended while the epigaeic ones disappear. In con-

trast, the basal columns of *burchelli* are always epigaeic all the way back to the bivouac. Compared with the raids of *burchelli*, the raids of *praedator* are usually much smaller, shorter in duration, more frequently nocturnal, and more often meander and double back over the area just raided. Although raids of *burchelli* may begin at dawn and occasionally last until somewhat past sunset, they never start during the night like those of *praedator* which can be found at any hour. *L. coecus*, which appears to be closely related to *praedator* morphologically, has epigaeic raids almost exclusively at night with a raid pattern intermediate between swarm and column types.

Although no detailed study of the prey has been made, numerous observations indicate that species of army ants when raiding in the same places may attack different species of booty. All species of army ants studied captured more ants than any other kind of prey but never captured any species of Ecitonini. The size of the prey species is somewhat correlated with the size of the army ant attacking it. However, there are cases where two species of army ants having workers of equivalent size differ in their attacks on potential prey. For example, *burchelli* readily and commonly attacks *Paraponera clavata* which appears to be avoided by *hamatum*. All species apparently kill more arthropods than they eat, and some species or groups of arthropods are probably never attacked or killed. None kill vertebrates frequently, as do certain Old World Dorylinae.

Bivouacs: All species of army ants probably have only temporary nests, called bivouacs, unlike the more or less fixed nests of most ants. The frequency or regularity of emigrations is unknown for most species. Epigaeic bivouacs are typical for only *E. hamatum* and *burchelli*, but the ability and habit of forming hanging clusters was found among other species of *Eciton* and *Neivamyrmex* even though their subterranean bivouacs do not consist primarily of such clusters. The legs of Ecitonini are relatively long and thick compared with those of most other ants, and these characteristics of the legs may be important adaptations for the clustering behavior. I do not believe the opposed recurved tarsal claws were developed with the evolution of such clustering because similar claws are present on many species of nondoryline ants including Ponerinae.

The epigaeic species of *Eciton* sometimes make a symmetrical

bivouac in the form of a cylinder or truncated cone on the inside or underside of a log. However, most epigaeic bivouacs are more complex in shape because they hang upon irregular cavities or brush heaps. Subterranean bivouacs of Ecitonini seem to have an even more complex shape and are usually subdivided into many small clusters because the ants use existing cavities with slight modifications and do not dig an entire nest or bivouac site. In contrast to the epigaeic species which keep their brood in the center of their relatively homogeneous bivouac, the position of the brood in subterranean bivouacs is much more variable. In addition, the species of *Neivamyrmex* in the United States apparently move their larvae, prepupae and pupae up to the underside of warm rocks during the day and shift the brood back into the soil when the rocks cool.

Refuse Deposits: All army ants presumably put dead ants and the remains of booty in refuse deposits a short distance from the bivouac. The refuse deposits of epigaeic species are the only ones which can be easily studied. There is little refuse outside colonies of *hamatum* because this species captures primarily softbodied insects. However, the refuse deposits of *burchelli* are extensive, containing thousands of living arthropods and sclerotized remains of arthropods. Most of the material in the refuse deposits is carried there by the workers, although some is dropped directly from the bivouacs. Most of the refuse is eaten or carried off by scavengers within a few days.

Emigrations and the Nomadic-Statary Activity Cycle: The emigration columns of *Labidus*, *Nomamyrmex*, and *Cheliomyrmex* sometimes are bordered by dirt walls or are completely covered by arches made of loose dirt by the workers. These walls or tunnels never were seen along the entire route but seemed to be constructed primarily where the ants left underground passages and moved on the surface of the ground. Exposure to light including direct sunlight did not stimulate the ants to build or extend these tunnels. *Labidus* and *Nomamyrmex* have been considered closely related on the basis of morphology, and this relationship is supported by the above behavior. *Eciton* and *Neivamyrmex* do not make walls of dirt along their columns.

Several additional cases are reported in which one species of army ant has followed for many meters a chemical trail made by another

species of army ant. However, little is known about the chemical nature of these trails and how they may affect the direction of raiding and emigration.

Scattered observations on various species support Schneirla's theory that the "condition" of the brood (primarily its age or properties dependent upon its age) is the most important factor influencing the start and duration of the nomadic phase (large daily raids and bivouac moved more or less daily for two to three weeks) and the statary phase (smaller less frequent raids and bivouac at one site for about three weeks). Although most species of army ants appear to have synchronous broods necessary for a precise nomadic-statary activity cycle, even with such broods, as Schneirla (1957b: 267-268) has pointed out, the cycle may not be as regular as that for *hamatum*. A nomadic phase with several nights without emigrations is typical of *Neivamyrmex opacithorax* and *nigrescens* which have synchronous broods. It is clear that *Labidus* sometimes has broods which are nonsynchronous or much less synchronous than those observed in *Eciton*, and the relatively large number of physogastric queens of *Labidus* which have been found may be attributed to a longer oviposition period than that of *Eciton*. It has been reported several times that bivouacs of *Labidus* remained in the same spot for several months or longer, but no information is available on the type of brood present in these bivouacs.

I agree with Schneirla's main theory that the brood or broods are the primary stimulus inducing raiding and emigrating; however, I believe he has gone too far in discounting the influence of the amount of booty on the activity of the ants. The amount of booty in an area affects the direction, distance, and duration of raids and emigrations. Although it has not been demonstrated, it would appear that the amount of food within bivouacs must influence the amount of activity of the larvae, and thus, their stimulation of the adults. As the larvae get larger, one might expect that since they presumably stimulate the adults more and also require more food, the distance that the ants raid and emigrate would increase. The total distance of raiding appears to increase among some species, but most of this increase results from raiding in several directions rather than in one direction from the bivouac. The emigration distances of *E. hamatum* and *Neiv. nigrescens* do not increase throughout the nomadic phase and may be greatest in the center of the

phase. Schneirla has emphasized several aspects of raiding behavior correlated with the caste and development of the brood.

Division of Labor and Integration: Some species of Ecitonini are exceedingly polymorphic, and the workers within a species often vary greatly in size and morphology. The following observations summarize rather incidental observations on the different castes and on workers of various sizes. The major workers of *Eciton* take part in the formation of hanging clusters and assist in capturing booty and attacking predators or any animal which disturbs a colony. A disturbance of a column of army ants or part of a bivouac often results in an increase in the number of majors at that point. Large workers of *Labidus coecus* were attracted apparently in a similar manner to the site of a struggle when smaller workers had difficulty transporting peanuts. These large workers assisted in dragging the peanut toward the bivouac. However, the largest workers of *coecus*, like those of *L. praedator*, probably do not leave the bivouac on raids. Compared with the largest workers of other genera of Ecitonini, the major workers or soldiers of *Eciton* both morphologically and behaviorally come closest to forming a distinct caste. The majors of *Eciton* were never seen to carry any booty or brood, not even the huge larvae of reproductives for which the large sickle-shaped mandibles of the majors might seem well suited. During emigrations the major workers are most abundant near the queen and make up a high percentage of the workers in the retinue accompanying her. When a bivouac of *Eciton* is torn apart, the queen is usually surrounded by a large number of excited majors. However, in an undisturbed bivouac the smallest workers usually form a tight ball around the queen.

Major workers were never seen being carried by any other workers, and the frequency with which workers are carried varies inversely with their size and age. Callow workers apparently do not take part in raids until at least a day and probably not until several days after they emerge. However, on the first nomadic emigration of *burchelli* a few callow workers carry cocoons or dark workers. The number of workers which are carried on an emigration increases toward the end of the emigration. Numerous workers which were being carried were collected, and all ran around actively and showed no sign of injury. When carrying adults or brood, workers typically placed their mandibles around the alinota of

adult workers, around the thoracic segments of larvae and around the posterior ends of cocoons. It was discovered that worker larvae of *Nomamyrmex*, like those of *Eciton* and *Labidus* spin cocoons. Worker larvae of *Neivamyrmex* do not spin cocoons. Queens of *Eciton*, *Neivamyrmex*, and *Nomamyrmex* were all observed running in emigration columns, and even physogastric queens of the first two genera were observed running. Workers running in the retinue of a queen were never seen to carry or pull the queen and probably hindered her movement much more than they helped her. The retinue increases the extent of an ant roadway in areas where the queen might have more difficulty running than the workers, and probably the retinue would protect the queen from a potential predator. The queen most commonly emigrates after three fourths of the colony has left the old bivouac but may emigrate after one third to one half of the workers have left.

Workers appear to be attracted more to the gaster of their queens than to any other part of her body. The workers rarely were attracted to the anal region or mouthparts. Workers were never seen to feed queens of *Eciton*, *Nomamyrmex*, or *Neivamyrmex*. Observations on single queens of these three genera suggest that the relative attraction of workers to the segments of a queen's gaster may be quite different depending upon the genus or species concerned as well as upon the individual.

The mating of one old *burchelli* queen in the laboratory supports the hypothesis that army ant queens mate more than once and may mate each year when sexual broods are produced. This is the third time mating by army ants has been observed. The shorter duration of copulation and the male's failure to strongly grasp the petiolar horns of the female were the main differences from the matings of *E. hamatum* observed by Schneirla. In both cases the males were weak and probably close to death following copulation.

Most male army ants probably live a few days and seldom live more than three weeks. It is likely that the males are photonegative and unable to fly for one to three days following their emergence and may become photopositive only after flight.

Relations with the Physical Environment: Schneirla's conclusion that males of *E. hamatum* and *burchelli* are produced in the dry season or dry periods is supported by additional records. Additional evidence is also given that males of *burchelli* are produced some-

what earlier in the season than those of *hamatum*. However, it is clear that queens of Ecitonini including some species of *Eciton* must lay eggs during the rainy season (and not during dry spells within the rainy season) which develop into reproductives. Some other factor such as possibly the onset of the rainy season or changes in day length must play a part in the production of the sexual broods.

Except for changes in behavior when broods of reproductives are in colonies, there do not appear to be any distinct differences in raiding or emigrating between rainy and dry season conditions for the epigaeic species of *Eciton*. The subterranean species of army ants more frequently have diurnal raids and emigrations on the surface of the ground on cloudy, humid, or rainy days than on sunny dry days. Thus, these species are more commonly seen during the rainy season than during the dry season. One exception seems to be *Neivamyrmex postcarinatus* Borgmeier, a species known only from Barro Colorado Island where it was found five times during the dry season but was not seen during the rainy season. The hypotheses of Schneirla concerning the effects of light, temperature, and humidity on the beginnings of raiding, the siesta period, and emigrations appear to be reasonable but are probably overly simplified. No one has simultaneously recorded fluctuations of these environmental factors and correlated them with the ants' behavior.

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Geographic Variation of Alate *Pemphigus populi-transversus* in Eastern North America [1, 2]

BY

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ABSTRACT: This paper examines the geographic variation and covariation of 18 morphological characters of the gall-making aphid, *Pemphigus populi-transversus*, in eastern North America. Samples of 15 galls from each of 23 localities ranging from Massachusetts to Kansas and Wisconsin to Florida were employed in the study. The present analyses are based on work presented in a companion paper (Sokal, 1962) in which intragall, intefgall and interlocality covariation had been separated. Maps of the geographic variation for each of the 18 characters are shown in Figures 3-20. Locality means have been transformed to probits for ease of comparison. A variety of geographic variation patterns is exhibited. Differences among localities are tested by means of a multiple comparison test after analyses of variance had been per-

1. Part 3 of a study of variation in the aphid genus *Pemphigus*. Part 1 is Sokal (1952), Part 2 is Sokal (1962).

2. Contribution No. 1130 from the Department of Entomology of The University of Kansas, Lawrence, Kansas.

3. Work for this study commenced as early as 1949 when the senior author was a graduate student in the Department of Zoology of the University of Chicago. He has continued at it intermittently since becoming a member of the staff at the Department of Entomology of The University of Kansas. A diversion of his interests prevented completion of the present study until this time.

The senior author is indebted to Professor Alfred E. Emerson of the University of Chicago for acquainting him with *Pemphigus*, for generous encouragement and for stimulating discussions on biological problems. Early aspects of this work were made possible by the Chicago Natural History Museum, whose fellowship the senior author held from 1948 to 1950. To Mr. Rupert L. Wenzel, Curator of Insects and Mr. Henry S. Dybas, Associate Curator of Insects of that institution goes sincere appreciation for space, facilities and counsel unstintingly offered.

Later work on this paper was carried out at the Department of Entomology of The University of Kansas, where Professor Charles D. Michener encouraged this work in numerous ways and has provided valuable counsel and criticism over the years. Some of the computations were performed (in 1952) at the former IBM facilities of the Guidance Bureau of The University of Kansas where Mr. Donald K. Ottman was free with advice and instruction. Our appreciation goes to Mrs. Julie C. Sokal who helped in many ways in advancing the present study. Mrs. Maxine L. Howe assisted with the computations and Mrs. Ann Schlager has drawn the maps.

The more recent aspects of this work have been supported by the University of Kansas General Research Fund. The junior author completed this study during his tenure of a predoctoral fellowship of the Division of General Medical Sciences, United States Public Health Service.

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formed. The results of the multiple comparison tests are shown as a series of partially-overlapping lines in the right lower corner of the figures and also by differences in shading of the maps. By means of a multiple factor analysis carried out in the companion paper (Sokal, 1962), three factors determining interlocality correlations were isolated. Information on character variation can be condensed by plotting the geographic variation pattern of each of the three factors (Figures 21-23). The possibilities for categorization of subspecies are discussed on the basis of these findings and are illustrated in Figure 24.

INTRODUCTION

This paper is a study of the geographic variation and covariation of 18 morphological characters of the aphid *Pemphigus populitransversus* Riley in samples from 23 localities in eastern North America. In an earlier work Sokal (1952) examined 21 characters of a single local population of this gall-forming aphid from Ripley, Ohio. The present study is related to a companion paper (Sokal, 1962) in which the variation and covariation of the characters of the present study were analyzed in some detail. In that study all but one character differed significantly among localities. Patterns of covariation differed at the three hierarchic levels of variation in the analysis, these levels being variation of alates within galls, variation of galls within localities and variation among localities. The covariation matrices were resolved by multiple factor analysis and simple structure matrices were obtained for each of the three levels of covariation. The results of the factor analysis at the interlocality level will be discussed below in connection with the description of geographic variation.

The present study was undertaken not only with a view to learning more about the systematics of the genus *Pemphigus*, but also in an attempt to see what light the variation patterns in *Pemphigus* can throw on the general problems of geographic variation. In recent years considerable controversy has raged about methods of describing infraspecific variation in animal populations. Some of the many references on this problem, which has become known as the subspecies controversy, are (in chronological order) Wilson and Brown (1953), Edwards (1954), Gosline (1954), Mayr (1954), Sibley (1954), Hubbell (1954), Brown and Wilson (1954), Fox (1955), Sabrosky (1955), Durrant (1955), Doutt (1955), Edwards (1956), Gillham (1956), Smith and White (1956), Hagmeier (1958), Christiansen (1958), Burch and Thompson (1958), and Pimentel (1958, 1959). Points of view in these arguments have been largely presented on *a priori* grounds and it is urgent to weigh the merits of the various views presented on the basis of pertinent evidence. A critical argument in the subspecies controversy is the problem of

concordance and discordance of characters, which can only be illuminated by the study of the variation of many characters among populations of the same species. The data at hand are well-suited for such an analysis.

The second important reason for studying the geographic variation of many characters is that geographic variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is doubtless a multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and ranges probably overlap in rather complex fashion. It is therefore necessary to study the variation as well as covariation of many characters.

The present study is part of a larger investigation including a total of 76 localities in eastern North America, comprising varying sample sizes (Sokal and Thomas, 1963). For these other localities fewer alate characters were recorded than in the 23 localities reported below. The present data are analyzed and published separately, because (1) they are closely tied to the companion study (Sokal, 1962); (2) they permit the simultaneous treatment of a greater number of characters; (3) owing to equal sample sizes at every hierarchic level, they permit the testing of various methodological devices for the analysis of geographic variation patterns without the complications necessitated by formulae adjusted for differing sample sizes.

It may occasion some surprise that the statistical problems involved in the analysis of geographic variation have been almost untouched in spite of the amount of emphasis that has been given to this subject as a cornerstone of the New Systematics. With the exception of the valuable papers by Pimentel (1958, 1959), directions for statistical analysis of such data have been either erroneous or lacking altogether. There is therefore a strong methodological emphasis in the present paper. It is hoped that these techniques will be interesting and valuable to students of geographic variation of diverse organisms. Attempts at a biological interpretation of the geographic variation of *Pemphigus populi-transversus* will be made in a subsequent publication, based on all available data, including also variation of stem mothers, which is not considered here.

MATERIAL

Sokal (1952) has outlined the rather complex biology of these aphids, which form galls on petioles of the cottonwood, *Populus deltoides*, as the primary host and migrate to the roots of herbaceous

plants in the summer. In the present study only alate fundatrigeniae were used and, whenever employed, the term alates refers to such winged forms only.

The 23 localities studied were chosen because they contained 15 or more galls of at least two alates each or, when several such localities were available in a given general area, because of their relatively equidistant position from other localities. Figure 1 is a map of the eastern United States with the chosen localities plotted. The localities and the dates of collection are listed in Table 1. Localities 18, 19 and 20 each contain several small samples from the general areas Northern Florida-Georgia, Kentucky-Tennessee, and Arkansas, respectively, because no single locality provided 15 galls with two alates each. Where more than the required number of galls and alates were available in any one locality, 15 galls were selected at random, several alates from each gall mounted on slides and two alates per gall chosen at random for measurements.

The 18 characters studied and methods of measurement have been described in detail in the earlier papers (Sokal, 1952; Sokal, 1962).

DESCRIPTION AND ANALYSIS OF GEOGRAPHIC VARIATION

As a first step in the analysis of geographic variation the descriptive facts have to be summarized in some convenient way. This is best done by separate maps for each character, showing the means of the populations at the various localities. These means were obtained from the computations of the companion study (Sokal, 1962). The means for the 18 characters at all localities are listed in Table 2 as millimeters for continuous variables and as counts for meristic characters. Since the means are all based on the same number of individuals and an analysis of variance of all localities had been performed, we furnish the average standard error within localities at the bottom of each character column, instead of attaching a separate standard error to each mean. This average standard error suffices for any significance testing desired.

In plotting these data on distribution maps we find it advisable to transform the original scale of measurement by standardization because this will simplify comparison of maps representing different characters. Standardization of each locality mean is carried out by dividing its difference from the grand mean of localities by the standard deviation of locality means. When this is done, localities

whose means are less than the grand mean will have negative scores in standard deviation units. In order to avoid this somewhat unfortunate scale for mapping, we have taken the customary approach of changing standard scores to so-called probit scores by adding a constant 5.0 to them. Thus a locality with a mean identical to the grand mean of the study will score 5.0, a locality with a smaller mean will score below 5.0, and a locality with a mean larger than the average will score above 5.0. A final step for simplifying the maps has been to multiply all probit scores by 10 to avoid decimal points. Thus a probit value of 5.3 is mapped as 53.

Brief accounts of the geographic variation patterns of each character follow, illustrated by Figures 3 through 20. Even cursory study will show that there are fewer than 18 variation patterns repeating themselves (with some modification) for the various characters. *In examining the patterns of variation in Figures 3 through 20, the shading of the areas* (conventions explained in Figure 2) *is to be ignored at this stage in our discussion.*

Forewing length (Figure 3). This character shows two areas of low mean values, one in the western half of the area studied, the other in New England, New York and Pennsylvania. An area of high means is present in Ohio and west of the Applachians, extending southeast into northern Florida.

Head length (Figure 4). The locality with the lowest means is near Kansas City. There is a central area of low values representing in a general way the Mississippi River Valley and extending southeast into northern Florida. High means are generally found in the north, with the highest means concentrated in western Ohio and northern Indiana. There is some extension of this high area into Iowa and south central Kansas.

Head width (Figure 5). The general variation pattern of head width resembles that of head length quite closely. The lowest mean is again near Kansas City. However, the area of low means does not extend to the Southeast for this character.

Thorax length (Figure 6). This measurement shows some of the features of both wing length and head length discussed above. There is an area of low means ranging from Illinois to southeast Kansas and extending as far south as Arkansas. The high means cluster in Ohio and Indiana and include the Georgia-Florida area. All other localities are intermediate in magnitude.

Thorax width (Figure 7). We find again an area of high means

in Ohio, Indiana and Georgia-Florida; low means are restricted to Missouri, Arkansas and southeast Kansas. Other areas are intermediate in magnitude for this character.

Femur length (Figure 8). This variable has low means in all localities west of the Wabash and lower Mississippi River. A low area occurs also in northern Pennsylvania. The high mean scores are again concentrated in Ohio and Indiana, as well as Georgia-Florida. Southern Iowa is also relatively high. The patterns of *tibia length* (Figure 9) and *tarsus length* (Figure 10) are quite similar to that of femur length discussed above.

Antennal segment III length (Figure 11). This character is similar in its geographic variation to the last three characters, except that the area of high means now includes central Illinois and excluded southern Iowa. *Antennal segment IV length* (Figure 12) shows a pattern similar to that of length of antennal segment III, with the trend of a high mean in central Illinois reinforced. In *antennal segment V length* (Figure 13) this trend continues and extends to the Kentucky-Tennessee area.

Antennal segment VI length (Figure 14). This character appears to exhibit a general north-south trend; there are high means in the north and low means in the south.

Number of sensoria on antennal segment III (Figure 15). This variable shows a peculiar distribution, with low values in the south and extreme north, highest values in Ohio and a band of high values extending west through Illinois and Iowa.

Number of sensoria on antennal segment IV (Figure 16). We find a variation pattern somewhat similar to that of the character just discussed. There are high values in northern Ohio and in central Illinois, but not in Iowa. There is one high mean in the Hudson River Valley.

Number of sensoria on antennal segment V (Figure 17). The highest means are in Ohio with fairly high values in New England and Iowa and low values in the south and north and also in southern Ohio. *Number of sensoria on antennal segment VI* (Figure 18) resembles the previous character in its variation pattern, except that the locality in southern Ohio now has a high mean.

Number of sclerotic islands in the primary sensorium of antennal segment V (Figure 19) has low values in New England, northern Pennsylvania, southern Indiana, and southeastern Kansas; high values in northern Ohio and intermediate values elsewhere.

Number of sclerotic islands in the primary sensorium of antennal segment VI (Figure 20). This character has a band of high means extending through New York, Pennsylvania, Ohio, Indiana, Illinois, and Iowa into central Kansas with low values north and south of this line. The lowest mean, however, is in the Florida-Georgia area.

For geographic variation of this sort two major formats of representation have been customary. The first has been the so-called "Dice-grams," which are graphs showing the means of measurements of different populations and their standard errors. This scheme was first proposed by Dice and Leraas (1936). It has been adopted by a number of authors and modified by Hubbs and Perlmutter (1942), Hubbs and Hubbs (1953), and Pimentel (1958). In spite of its wide-spread acceptance it has a number of disadvantages. It is difficult if not impossible to follow any geographic trends with Dice-grams except in the case of linear geographic variation, as along a shore line or a river, or when dealing with a single clinal transect through a geographic area. Extensive studies involving many localities would be quite difficult to include in a single diagram per character. A more serious drawback to Dice-grams are the erroneous implications for statistical testing commonly drawn from them. The presentation of standard deviations of samples and of means tacitly suggests that ordinary levels of significance apply to this work, *i. e.*, that *t* tests for pairs of these localities would be appropriate. This is not so, because on the one hand the tester is not taking advantage of the opportunity of improving his error estimate by pooling the variances of all his samples, concomitantly obtaining a greater number of degrees of freedom (steps which would raise the level of significance of tests to be applied); and on the other hand because systematic testing of all comparisons in a study cannot be done using the random sampling assumptions of simple *t* tests.

A second method of representation has been the drawing of geographical variation maps showing the magnitude of the means of a given character for all localities and delimiting areas of equal magnitude by so-called isophene lines. These areas generally form orderly patterns of variation for each character. Very little is said in the literature about the art or science of drawing isophene lines. The general problem concerns the definition of criteria for perceiving order in a system of values varying in two dimensions. We have considered this issue for some time without coming to any very satisfactory solution so far and we would like to direct the attention

of statistically-minded taxonomists to this very real problem in the study of geographic variation. If the geographic variation follows a reasonable simple pattern and if many localities have been studied, drawing isophenes will not be particularly troublesome. The fewer the localities that have been studied the more unreliable isophenes must necessarily be.

A first point in the description of patterns of geographic variation must be the demonstration of the nonrandom distribution of the locality means in the area studied. Seemingly random distribution of significantly different means in a population could be possible under certain rather specialized assumptions. To the knowledge of the writers no actual distribution of this kind has been described to date. In the great majority of animal and plant species, one should expect adaptation to geographically-varying factors and the absence of complete panmixis; hence these forms should exhibit more or less orderly differentiation. However, disturbances are likely due to unknown ecological factors possibly present in crazy-quilt patterns, or to unknown historical phenomena, such as migrations, as well as chance phenomena of various sorts.

A group of n localities distributed equidistantly over an area may serve as a model. If we have n means of a variable ranked in order of magnitude and allocate them at random to the n localities, what possible patterns of variation, seemingly meaningful biologically, could be generated by chance alone? A possible test for nonrandomness of distribution might be the statistical method of runs. For example, if the means are ranked in order of magnitude from the highest to the lowest all means above the median can be assigned plus signs, all those below the median minus signs. Starting with the highest mean one might show that the next five or ten means geographically closest are of like sign. If fairly large number of means are involved only the first and the fourth quartile might be employed for the + and — groups, respectively. On the assumption of equal occurrence of + and — localities, five neighbors of like sign will occur with a probability of only 0.018, hence below the customary level of significance. Attempts to apply this method to our study were not too successful. For example, in the character forewing length (Figure 3), locality number 22 in the southeastern corner of Indiana has the highest score (68). The six localities closest to it are all of like sign, hence give an indication of a nonrandom distribution. On the other hand, had we started with locality number 9 in eastern Ohio, which has an equally high mean, the fifth closest

locality would have been locality number 4 in western New York, which is of unlike sign. A similar attempt was made to test for runs starting with the localities of lowest means, *i. e.*, number 15 near Kansas City or 17 in southeast Kansas. The five means closest to them are not of like sign, because of the rather complicated patterns of geographic variation in this character. It is clear that the method will be relatively less successful the fewer localities are included in a study; also if one of the extreme values is found near a boundary line or a major zone of transition the runs method is likely to fail. Yet rough nonparametric tests of this general nature might be suggested, if relatively clear-cut patterns of geographic variation seem present.

The analysis of geographic variation was carried out as 18 separate hierarchic analyses of variance, one for each character. The details of this method have been described in the companion paper (Sokal, 1962), in which variances for each character were partitioned into components representing sources of variation at the intragall, intergall and interlocality levels. For our present purposes only the interlocality level need be considered.

In studies of geographic variation the analysis of variance can be considered from two conflicting yet legitimate points of view. The separation of analysis of variance into at least two models, fixed treatment effects (model I) and random effects yielding variance components (model II), is well established. In model I we attempt to assess the effects of deliberately chosen treatments. If the over-all analysis shows significant differences among treatments, we generally make separate comparisons of pairs of means to understand the relationships between the treatments. In a model II analysis of variance we are not interested in comparing the effects of the treatment on the means, since the treatments are chosen at random. Instead we measure the contribution to the over-all variance of the various sources of variation. In the earlier paper (Sokal, 1962) the analysis had been interpreted solely as model II. The 23 localities were considered to be chosen at random from among the many other localities which might have been chosen. This point of view is in fact quite legitimate, since more localities were available for study and many more samples could have been obtained with further field work. The model II analysis permitted an evaluation of the relative effects of the various levels of variation on the over-all variation of each character.

In the present study, however, the same 23 localities are now

regarded as fixed treatments in the sense of the analysis of variance. Attention is now focused on the pattern of geographic variation rather than on amounts of variation; we wish to estimate differences in means between pairs of localities and test these for significance. We are thus in the unusual situation of employing the same analysis of variance in two separate and superficially contradictory endeavors. Such a procedure is generally proscribed in statistical texts and would rarely occur in the customary problems of experimental design. This is but one of the peculiarities of data in systematics to which little attention has so far been drawn. Statistical theory has been developed almost exclusively in response to the needs of scientists other than taxonomists. Consequently the taxonomist has had to content himself with methods fashioned primarily for other purposes.

The model II analysis of variance (Sokal, 1962) showed that all characters except sensoria VI exhibit significant interlocality variance.* The percentage of interlocality variance varies with the character, ranging from 54 percent for forewing length to 4.8 percent for sensoria V. In general the continuous characters have a higher percentage of interlocality variance than the meristic characters. Since the computational procedures and tests of significance for models I and II analysis of variance are identical, significant differences are found among locality means of all characters except sensoria VI.

Tests between means at any two localities were carried out by means of multiple comparisons tests. It has already been stated that the application of ordinary t tests to such data, although a widespread practice in taxonomic work, is not legitimate. A great variety of multiple comparison tests have been developed in recent years (see Federer, 1955, or Steel and Torrie, 1960 for some of them). The use of any of the multiple comparisons tests in studies of geographic variation is relatively new. Following suggestions from the senior author, such methods were applied by Cross (1955) in a study of geographic variation of bees of the subgenus *Epinomia* and by Ehrlich (1955) in a study of the butterfly, *Erebia epipsodea*. Pimentel (1958) has also recommended their use; we are unaware of any other application of these techniques. All multiple comparison tests array the means in order of magnitude and delimit mutually exclusive or overlapping sets of means, which within a set are

* In the interest of brevity, we shall use abbreviated names such as antenna III for antennal segment III length, sensoria III for number of sensoria on antennal segment III and islands V for number of sclerotic islands in the primary sensorium of antennal segment V.

not significantly different. When sets are mutually exclusive, boundary lines can be drawn easily. A test attempting to establish such groups is the so-called gap test (see Federer, 1955, p. 42). However, since this test is extremely conservative, it would fail to show differentiation in many cases where the analysis of variance indicates significant differences among a group of means.

We adopted the Student-Newman-Keuls (SNK) test (Steel and Torrie, 1960) for the present analysis, because it yielded relatively less overlap and hence more differentiation among the sets than other tests resulting in partially overlapping sets of means such as Tukey's "honestly significant difference" test. The results of the SNK test are shown graphically along the right hand margin of Figures 3 through 23. These diagrams show the 23 locality means for any given character arrayed in order to magnitude from lowest to highest. Lines to the right of the array define sets of not significantly different means. Any two means not connected by a single line can be considered to be significantly different from each other at $P \leqslant 0.01$. Thus in Figure 3 (forewing length) means 37 and 41 are not significantly different from each other, while mean 37 is significantly different from mean 48. Means 58 through 68, which are not significantly different from each other, are significantly different from all means below them, there being a gap, *i. e.*, no overlap, between the highest set and any of the low ones.

The conventions used for differentiating levels of means on the distribution maps (Figures 3-23) were based on the SNK tests. Guidelines in establishing the conventions for drawing the maps were the following: there should be some indication of relative magnitude of means by shading; there should also be some indication of significance of differences between adjacent areas. Because of overlapping sets this proved to be a difficult task indeed and several schemes were attempted and rejected in turn. The scheme adopted by us proved the least objectionable of the ones that we were able to develop. We would gladly welcome suggestions for its improvement.

Figure 2 explains in schematic form the shading conventions employed as a result of the SNK tests. An attempt was always made to find nonoverlapping low and high groups of means. The low group was dotted (grey shade when reduced and reproduced), the high group crosshatched. Where an intermediate level group was present this was represented by diagonal hatching. Whenever adjacent groups were separated by a gap so that all members of one

were significantly different from all members of the next group a barbed line was drawn between the shaded areas. This is shown for example in Figures 2a, 2b, and 2f. Problems arose when lines representing sets of homogeneous means overlapped. In those cases where the low and the high groups did not overlap, this problem was solved by first defining the two end groups, shading these as indicated above and then assigning all intermediate means to the intermediate group. This intermediate group could be partially overlapping with one or both of the end groups as shown in Figures 2b and 2c, respectively, or it could contain several intermediate groups staggered, as indicated in Figure 2d or shown much more profusely in the diagram for the character antenna VI, Figure 14. Although no more than a single gap was found for any one character, four or more nonoverlapping groups of means could have occurred. In such a case more than three shadings would have been necessary to represent the situation. Where only two contiguous but nonoverlapping groups exist a barbed line is shown between the two groups because every member of the low group is significantly different from every member of the high group (Figure 2f). The case in Figure 2e differs by having an intermediate group overlapping both the low as well as the high group. Since therefore not every member of the low group is significantly different from every member of the high group, no barbed line separates the two nonoverlapping end groups. When there is overlap between the high and the low groups (Figures 2g and 2h), regardless of whether there are intermediate groups present, we have designated the area of overlap as intermediate although it is different in nature from the intermediate class of the earlier examples. At one time we planned to distinguish this type of intermediate area by a separate kind of shading, but abandoned this idea in order to keep the conventions as simple as possible. If significance tests are desired these can easily be performed visually by comparing the means on the map with the SNK diagram furnished alongside it. Finally Figure 2i shows an undifferentiated example, where no significant difference can be shown among any of the means in the study. Two such cases were found in the present study. We have arbitrarily coded all such means as belonging to a homogeneous low group.

An understanding of the meaning of the shading conventions will enable the reader to follow the trends in Figures 3 through 20, outlined earlier in this section more thoroughly. While the previous

descriptions were based on the means alone, these are born out by the patterns of shading on each map.

DESCRIPTION AND ANALYSIS OF GEOGRAPHIC COVARIATION

Correlations

The structuring of the data into three levels of variation permitted the construction of three covariance matrices (intragall, intergall product-moment, intergall component, interlocality product-moment and interlocality component), for each of the 18 characters, corresponding to the partitioning of the variances. The only matrix pertinent to the present study is the interlocality component correlation matrix, the computation of which is described by Sokal (1962) and which is shown in Table 4 of that paper. The interlocality component correlations lack sensoria VI because of the nonsignificance of the interlocality variance components of that variable. Interesting features of this correlation matrix are the high mutual correlations among the wing, thorax, leg and antennal measurements (except antenna VI, which is quite independent of these measurements, but is correlated strongly with the dimensions of the head). There is some correlation of the meristic variables among themselves and with other continuous variables.

Next we examined the correlation matrix in order to find a smaller number of dimensions of variation that would be adequate to represent the covariation present. By this means we hope to find a simpler way of representing interlocality correlations, as well as showing which independent interlocality patterns of variation exist in the study. By showing which characters are affected by the same dimension of variation on an interlocality basis we might arrive at an understanding of the nature of the adaptive trends in this study.

Factor Analysis

With the exception of the work of Jolicoeur (1959), no attempts are reported in the literature at summarizing the geographic variation of separate characters through fewer variation patterns than those represented by the number of the characters studied. Crude methods, such as cluster analysis (see Sokal, 1962, Figure 4) can be used to try to group characters around the primary sources of variation. More sophisticated approaches involve various types of multivariate analysis. The method chosen for this particular study was multiple factor analysis of the interlocality correlation matrix

with rotation to simple structure. The technique is described in some detail by Sokal (1962). Other recent applications in related fields are described by Rohlf and Sokal (1962), Sokal and Daly (1961), Sokal (1958a) and Stroud (1953). Briefly stated, factor analysis is a branch of multivariate statistics which, in examining a complex set of phenomena, attempts to express these in terms of a few underlying factors explaining a large part of the variance of the original observations. The raw material of a factor analysis is generally a matrix of correlation coefficients. Factors which emerge from such a study are hypothetical constructs which can frequently be shown to possess objective reality, either through reappearance in successive factor analyses of similar material (invariance), or by positive identification as known causal factors. The results of a factor analysis are presented either in tabular form (*e. g.*, Sokal, 1958b, Table 11) or by means of arrow diagrams (*e. g.*, Sokal, 1958a, Figure 2).

The results of the factor analysis of interlocality component correlations are shown in Table 3. On the right-hand half of the table, pattern coefficients are expressed as plus or minus signs instead of absolute magnitudes. Only coefficients $\geqslant /0.55/$ are shown there. Three major common factors are evident. Factor I is an antennal sensoria factor affecting sensoria III and IV, as well as islands V and VI. Factor II affects the head, thorax, legs, antenna VI and sensoria V, while factor III appears to be a general size factor, including wing, thorax, legs and antennal segments III to V.

One may attempt to represent these factors by single characters. Criteria for choosing such a character would be that it be strongly affected by the factor in question and only slightly by any other factor. Such decisions are best not made on approximate pattern loadings as represented by the plus and minus signs, but on the original pattern coefficients shown in the left half of Table 3. Sensoria IV represents factor I best, while head length appears to be a suitable character for factor II. Wing length should be chosen to represent factor III. An examination of Figure 16, 4 and 3 will show that these three characters do indeed represent divergent trends among the various geographical patterns which can be observed in the characters studied. Factor analysis also explains some of the intermediate patterns as, for example, the geographic variation of thorax length (Figure 6) which is a strong reflection of both factors II and III and therefore is intermediate in its geographical pattern.

However, the representation of a factor by a single character is not an ideal procedure. Not only does each chosen character reflect in small measure the effects of other factors, but also, unless the character is totally determined by the common factors, it will represent a certain amount of variation due to its specific factor. The "specific factor" is a catch-all term for all the unknown and unaccountable sources of variation on each character other than the common factors which the factor analysis has isolated. A measure of the proportion of the variance of a character due to common factors is the communality seen in the column labeled h^2 in Table 3. The larger the communality of a character, the smaller the proportion of the variance determined by its specific factor. Thus we would aim to represent the factors by characters with high communalities. Since this is not always possible, it is often better to define a factor by means of more than one character.

The problem here is similar to that faced by the users of factor analysis in educational research, who after having given a large battery of tests to a group of individuals and having estimated the factors which account for the correlations among these tests, desire to find the factor endowment of any given individual by giving him only a few of these tests. One procedure is to use several tests which have high factor loadings on the desired factor and to average the scores of these tests on the assumption that the fluctuations due to specific factors would cancel each other. We have adopted this procedure and have used the following three groups of characters to identify the factors. To represent factor I we have used sensoria III, sensoria IV and islands V; to represent factor II we have used head length, head width and antenna VI; factor III is represented by forewing length, tibia length and tarsus length. Averages of the standardized scores of the three characters for each factor were computed for each locality and plotted on maps (Figures 21, 22 and 23). Estimated variances of galls within these means were computed, based on expected variances of sums of variables and allowing for the correlations between the variables composing the average score of each factor. With these estimates of the variance, SNK tests were applied to the average scores for the localities. Diagrams for these SNK tests are furnished in the customary manner at the lower right corners of Figures 21 to 23.

Examination of the geographic distribution of the average scores reveals three distinct patterns of geographic variation. Factor I (see Figure 21) produces a small area of high means in northern

Ohio involving localities 5 and 6. This area is significantly different from all other areas of the study, as is shown by the barbed line surrounding it. A narrow band of intermediate localities extends westward from the Ohio area with intermediate scores in locality 11 in Illinois and 13 in Iowa. Existence of this band is somewhat problematical. Faced with the necessity of accounting for intermediate level scores at these midwestern localities and basing our judgment in part on the presence of other localities in the same area which showed intermediate levels for various characters loaded on factor I, such a band was drawn. It may be, however, that no band exists and that the situation would better have been represented as two enclaves in the otherwise entirely low-level area surrounding these localities. Factor II exhibits high scores in the northern half of the study area (Figure 22). Low-level localities occur near the center of the area (in Kentucky-Tennessee and in Arkansas and near Kansas City). Intermediate level localities are in Kansas and in the Georgia-Florida area. Factor III has a high area in northeast Ohio extending into southwest Ohio and southeast Indiana with some indication of another high in the Georgia-Florida area. All low localities are west of the Mississippi and Wabash Rivers but two localities in the northwest (in Iowa) are again of intermediate level, as are localities in the northeast. An attempt was made to represent factor III by averaging scores for six characters, adding to the three considered above the length of antennal segments III, IV and V. Locality 3 in northern Pennsylvania, intermediate in Figure 23, became low level, indicating some depression of the mean in this area. Otherwise the geographic variation pattern of factor III was unchanged.

DISCUSSION

Procedures for the Study of Geographic Variation

Two main innovations have been proposed above for the study of geographic variation. The first is the testing of significance using a multiple comparisons test after an analysis of variance and the second is the reduction by factor analysis in the number of variables needed for study. There is little doubt that the former procedure is appropriate. The tests recommended in the general literature are all *a priori* tests and would therefore over-estimate significance levels when applied as part of a consistent testing procedure of every locality against every other locality, as is often done or at least implied.

Pimentel (1958) has given an account of the misunderstandings which have arisen on the application of the so-called "percentage" rules for recognizing distinct populations. These rules advocate separation based on the ability to distinguish from 75% to 90% of the populations concerned. Pimentel advocates an 84% mutual non-overlap between two populations as a requirement for the recognition of their subspecific status. While the formulation of the percentage rule by Pimentel is superior in logic and consistency to previously suggested ones, we would question the rationale of the entire procedure on the following grounds:

1. Such a procedure confuses the measurement of differences (one of the aims of the study of geographic variation) with probability statements about the significance of such differences (an issue of secondary importance).

2. As already stated, systematic testing would involve the studentized range; ordinary sampling distributions based either on the normal or t distribution would not be applicable. Hence the customary percentage rules would yield inaccurate separation. Most of the statements found in the literature (and admittedly the SNK test) are based on indefensible assumptions of equal variance among localities and may actually disguise situations of great interest.

3. The entire approach of the so-called percentage test puts emphasis on separating and naming populations rather than on the description of the variation as it exists. Excessive zeal in this direction has led to some of the reaction against subspeciational work in recent years.

4. Even should the pattern of variation and differentiation found by the percentage rules represent relatively correctly the situation for a given character, it may not do so for other characters. If subspecies are to be described on the basis of numerous characters, they must represent clusters of forms in a hyperspace bounded by separate co-ordinates representing the various characters.

Except in cases of ample collections, numerous localities and homogeneous variation patterns, the drawing of accurate and meaningful isophene lines on maps would present serious problems. The system adopted here, based on SNK tests of the means has a number of drawbacks. When different studies are compared, as for example in the extended study of the same species to be published soon (Sokal and Thomas, 1963), the shading of the areas in maps of different studies will not necessarily coincide. This is to be expected

since the division of the areas is based on tests of significance and not on absolute limits of isophenes. Class intervals for each type of shading differ also from character to character. The coding of localities as probits presents similar problems, since absolute magnitudes cannot be compared in different studies. The coding in probits is based on the standard deviation among means within a study; hence addition of new localities to a map must result in a new coding system. However, this should not prove too serious an impediment because comparisons are generally made within a given study and distribution map. For the characterization of infraspecific populations, the absolute measurements expressed in millimeters or counts should be employed.

The Application of Factor Analysis

The use of factor analysis in describing dimensions of variation common to a set of characters should become increasingly practicable with the ever growing availability and speed of electronic digital computers. Some surprise may be occasioned by the low number of common factors encountered in the present study. Are there really only three separate adaptive systems at work in the area under study? Common-sense inferences from biological theory and the organisms concerned would lead to a larger number of adaptive systems. Several explanations might be attempted. Blackith (1960) asserts that measurable morphological characters of insects represent only a relatively small number of independent patterns of growth. In such a case the various adaptations of the organism to the environments as reflected in the characters studied, could only be seen through adjustments in a few patterns of growth. Thus the present situation may correspond to a reaction system of many stimuli, but only three possible response variables, wherein all possible challenges to the system are met by adjustments in these three variables.

Another explanation for the paucity of factors would be that in measuring dimensions of the body we are not adequately sampling the genetic variation of the organisms, because some of the geographic variation is expressed through various other characters such as physiological, morphological or ethological ones which have not been measured. Undoubtedly there is some truth in this. However, one would expect that because of the complicated nexus of interrelations of cause and effect in the expression of phenotypes (Sneath and Sokal, 1962), pleiotropism and similar phenomena would cause some reflection of obscure morphological and physiological differ-

ences in the visible phenotype of the organism. In fact some of these differences may be reflected in the specific factors, although in the present study these do not appear to be very important.

It might also be argued that correlations are restricted to only three dimensions of variation in these data because there are only three geographically varying adaptative trends in this study. Many demands made on the organisms vary within localities and therefore do not show up on an interlocality basis. While this may be partially true, it is not likely to be a sufficient explanation of the paucity of factors.

In considering the number of factors it should be understood that we are only obtaining the major common factors in factor analysis *i. e.*, we attempted to keep the risk of overextraction of factors at a minimum. Thus there are undoubtedly other, less important, common factors present, which we cannot isolate and identify by our present methods.

Specific factors have not been considered in this study because, in the interlocality component matrix, communalities are relatively high (see Table 3, column labeled h^2). In other studies with some characters of low communalities, specific factors would have to be considered and would thus increase the number of factors necessary for an interpretation of geographic variation of the population. However, it will be remembered that in estimating the factor "endowments" of each locality three characters were employed per factor in the expectation that deviations due to specific factors for each character would cancel out.

Categorization of subspecies

A full discussion of the implications of the findings on *Pemphigus populi-transversus* for the subspecies controversy must wait until more extensive distributional data on alates as well as on stem mothers have been published (Sokal and Thomas, 1963). Certain conclusions, however, are already evident. If we wish to identify distinct infraspecific populations we could easily avoid redundancy by doing so on the basis of the factor analysis. A simple attempt is shown in Figure 24. Populations were characterized by using the low, intermediate and high levels of each of the three factors shown in Figures 21, 22 and 23. The combinations are identified by *i* for low level, *I* for intermediate level and *I* for the high level. The number of each factor is given by the number of symbols. Thus *i,II,III* means that factor I is present at low level, factor II at intermediate level and factor III at high level at a particular locality.

Nine of the 27 possible combinations occur in the 23 localities of the present study. Two combinations, *i,II,111, and i,ii,iii* occur repeatedly; the former appears to be a northern form existing in the northern portion of the area. The related forms *i,II,iii* and *1,II,111,* complete the northwest boundary. Form *i,ii,iii* occurs in the southwestern part of the study area. It will be remembered that the levels of the factors do not necessarily imply significant differentiation except in the case of factor I where the high level is significantly different from all others. However, the differences from *ii* to *II* and from *iii* to *III* are probably significant in most cases. Thus we see that even for so relatively limited a number of localities we could, should we so desire, describe several subspecies. When the number of factors is increased, more combinations could be described and possibly named.

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TABLE 1.—List of Localities Employed in This Study.

LOCALITY CODE NUMBER	Locality	Date
1	U.S. Hy. 1, 3 m. SE of Walpole, Norfolk Co., Mass.	12-VIII-1950
2	U.S. Hy. 6, 2 m. W of Goshen, Orange Co., N.Y.	11-VIII-1950
3	U.S. Hy. 6, 5 m. N of Wyalusing, Bradford Co., Pa.	10-VIII-1950
4	North Tonawanda, Niagara Co., N.Y.	15-VIII-1950
5	1½ m. SW of Laporte, Lorain Co., Ohio	10-VIII-1950
6	Perrysburg, Wood Co., Ohio	16-VIII-1950
7	Mishawaka, St. Joseph Co., Ind.	16-VIII-1950
8	Wis. Hy. 50, 5 m. E of New Munster, Kenosha Co., Wis.	15-VII-1949
9	U.S. Hy. 244, 3 m. W of Berlin Center, Mahoning Co., Ohio	3-IX-1950
10	Ohio Hy. 364 along Lake St. Marys, 3 m. SW of St. Marys, Auglaize Co., Ohio	29-VIII-1950
11	U.S. Hy. 24, 2 m. E of East Peoria, Tazewell Co., Ill.	11-VII-1949
12	1 m. E of Grandmound, Clinton Co., Ia.	23-VII-1950
13	Leon, Decatur Co., Ia.	24-VII-1950
14	U.S. Hy. 36, 5 m. W of Hull, Pike Co., Ill.	25-VII-1950
15	U.S. Hy. 24, 6 m. E of Kansas City, Jackson Co., Mo.	23-VII-1950
16	5 m. SE of Hutchinson, Reno Co., Kan.	2-IX-1951
17	U.S. Hy. 166, 11 m. E of Arkansas City, Cowley Co., Kan.	6-IX-1951
18	U.S. Hy. 441, 2½ m. N of Ocala, Marion Co., Fla., 2 galls	22-VIII-1949
	Poulan, Worth Co., Ga., 2 galls	29-VIII-1949
	U.S. Hy. 90, 3 m. E of Bonifay, Holmes Co., Fla., 3 galls	21-VIII-1949
	Sneads, Jackson Co., Fla., 3 galls	21-VIII-1949
	U.S. Hy. 19, 1½ m. N of Albany, Dougherty Co., Ga., 5 galls	30-VIII-1949
19	U.S. Hy. 70, 10 m. SW of Brinkley, Monroe Co., Ark., 3 galls	3-VIII-1950
	Flood plain of Arkansas River at Ft. Smith, Sebastion Co., Ark., 6 galls	3-VIII-1950
	U.S. Hy. 70, 8 m. W of Lonoke, Lonoke Co., Ark., 2 galls	3-VIII-1950
	Mississippi River bed, 1 m. W of the river and 8 m. E of West Memphis, Crittenden Co., Ark., 3 galls	3-VIII-1950
	U. S. Hy. 71, 1 m. N of Texarkana, Bowie Co., Tex., 1 gall	3-VIII-1950
20	U.S. Hy. 41, 1 m. NW of Adams, Robertson Co., Tenn., 4 galls	15-VIII-1949
	U.S. Hy. 41, at Guthrie, Todd Co., Ky., 4 galls	15-VIII-1949
	U.S. Hy. 60, 4 m. W of Kevil, Ballard Co., Ky., 3 galls	31-VII-1949
	U.S. Hy. 51, 5 m. S of Covington, Tipton Co., Tenn., 2 galls	3-VIII-1950
	U.S. Hy. 51, 1 m. S of Trimble, Dyer Co., Tenn., 2 galls	3-VIII-1950
21	U.S. Hy. 52, 4 m. SE of Ripley, Brown Co., Ohio	9-IX-1949
22	U.S. Hy. 52, in Dearborn Co., 6 m. SE of New Trenton, Franklin Co., Ind.	10-IX-1949
23	Gwynneville, Shelby Co., Indiana	10-IX-1949

TABLE 2.—Means of all characters for all localities.

LOCALITY CODE NUMBERS	Forewing length	Head length	Head width	Thorax length	Thorax width	Femur length	Tibia length	Tarsus length	Antenna III	Antenna IV	Antenna V	Antenna VI	Sensoria III	Sensoria IV	Sensoria V	Sensoria VI	Islands V	Islands VI
1.....	1.68	.20	.37	.56	.55	.46	.63	.14	.16	.063	.094	.177	3.27	.10	1.17	1.03	1.73	2.93
2.....	1.70	.21	.38	.56	.56	.47	.64	.14	.16	.066	.093	.178	3.47	.30	1.23	1.07	2.07	2.73
3.....	1.65	.21	.38	.55	.58	.44	.61	.14	.15	.061	.090	.176	3.30	.27	1.13	1.03	1.97	3.20
4.....	1.66	.21	.36	.56	.56	.46	.63	.14	.15	.064	.093	.179	3.37	.13	1.07	1.00	2.26	3.17
5.....	1.99	.20	.38	.59	.59	.48	.67	.15	.18	.075	.095	.170	4.83	.83	1.13	1.00	2.80	3.23
6.....	1.92	.21	.38	.60	.61	.48	.65	.15	.16	.068	.097	.175	3.73	.13	1.07	1.00	2.27	2.93
7.....	1.75	.21	.37	.57	.58	.48	.65	.14	.15	.064	.094	.180	2.83	.13	1.00	1.00	2.37	2.83
8.....	1.65	.21	.37	.53	.56	.44	.62	.14	.14	.058	.089	.175	3.07	.00	1.00	1.00	2.03	3.03
9.....	2.09	.20	.39	.63	.65	.52	.71	.16	.18	.076	.104	.179	4.03	.30	1.03	1.03	2.77	2.73
10.....	1.71	.22	.38	.56	.59	.46	.62	.14	.15	.064	.094	.179	3.53	.07	1.23	1.03	2.37	3.30
11.....	1.62	.21	.36	.51	.55	.44	.60	.13	.17	.072	.101	.173	3.90	.47	1.07	1.00	2.27	2.83
12.....	1.64	.21	.37	.53	.55	.44	.62	.14	.15	.062	.095	.179	3.63	.10	1.10	1.03	2.27	3.17
13.....	1.72	.21	.37	.56	.56	.47	.66	.15	.15	.064	.093	.184	3.93	.17	1.13	1.00	2.53	3.23
14.....	1.54	.20	.35	.49	.51	.41	.58	.13	.14	.056	.089	.168	3.37	.07	1.03	1.00	2.10	3.23
15.....	1.52	.19	.34	.44	.46	.40	.57	.13	.14	.057	.095	.172	3.47	.00	1.03	1.00	2.13	3.00
16.....	1.55	.21	.37	.52	.54	.42	.55	.13	.14	.055	.087	.165	2.27	.00	1.03	1.03	2.13	3.20
17.....	1.52	.21	.36	.50	.52	.41	.56	.13	.14	.060	.092	.170	3.33	.00	1.00	1.03	1.77	2.77
18.....	2.00	.20	.37	.58	.58	.49	.66	.15	.17	.070	.100	.164	3.00	.00	1.03	1.03	2.03	2.20
19.....	1.72	.20	.35	.50	.52	.42	.58	.14	.14	.063	.092	.161	2.53	.00	1.10	1.00	2.23	2.57
20.....	1.90	.20	.36	.57	.54	.46	.63	.15	.16	.067	.099	.166	3.43	.07	1.03	1.00	2.23	2.47
21.....	1.98	.20	.37	.56	.59	.48	.67	.15	.17	.071	.102	.172	3.83	.10	1.00	1.10	2.03	2.83
22.....	2.10	.21	.39	.63	.60	.51	.70	.15	.18	.070	.100	.172	4.17	.10	1.27	1.03	1.97	2.63
23.....	1.90	.21	.38	.60	.61	.48	.66	.14	.16	.066	.097	.175	3.43	.07	1.13	1.03	2.07	2.87
Average standard errors of means....	.039	.034	.051	.128	.139	.092	.123	.048	.036	.0166	.0173	.0264	.212	.055	.045	.032	.141	.164

All continuous variables are given in millimeters; all meristic ones as counts.

TABLE 3.—Primary Pattern Matrix for the Interlocality Component Correlation Matrix.

CHARACTERS	FACTORS I	II	III	h^2	I	II	III
Wing length	26	—05	81	79	.....	.....	+++
Head length	—18	94	—21	86	.....	+++	.....
Head width	—07	99	35	99	.....	+++	.....
Thorax length	—09	74	75	97	.....	++	+++
Thorax width	08	66	60	81	.....	++	+
Femur length	—04	65	83	1.02	.....	++	+++
Tibia length	10	53	79	93	.....	.....	+++
Tarsus length	32	30	72	85	.....	.....	++
Antenna III	43	16	79	1.00	.....	.....	+++
Antenna IV	47	06	79	99	.....	.....	+++
Antenna V	11	10	91	88	.....	.....	+++
Antenna VI	12	71	—19	64	.....	++	.....
Sensoria III	83	—11	27	77	+++	.....	.....
Sensoria IV	93	—10	08	82	+++	.....	.....
Sensoria V	05	66	13	48	.....	++	.....
Sensoria VI	X	X	X	X	X	X	X
Island V	76	—08	22	64	+++	.....	.....
Island VI	60	07	—88	1.01	+	.....	–––

Explanation: Plus or minus signs represent the following magnitudes of factor loading (positive or negative, respectively): 3 signs $\geqslant$ /0.75/, 2 signs $\geqslant$ /0.65/, 1 sign $\geqslant$ /0.55/. X signs mark variables not present in a given component correlation matrix. Decimal points have been omitted.

FIGURES 1-3

FIGURE 1.—Outline of the area studied with localities and their code numbers entered. Hollow triangles refer to area samples, solid triangles are locality samples. Numbers next to the triangles are the code numbers of the localities. The dashed outline constitutes the distribution of the cottonwood, *Populus deltoides* Bartr., according to the map of Sudworth (1934). From collection records by the senior author this map is not entirely accurate but in lieu of a more accurate map it has been accepted. The absence of cottonwoods from certain areas in Missouri and Iowa as shown on this map is questionable. The absence of cottonwoods from the Appalachian area has been verified by the author. Exact boundaries of cottonwood distribution near the Atlantic seaboard are not indicated since no samples from there were employed.

FIGURE 2.—Schematic diagrams showing the shading conventions employed as a result of the Student-Newman-Keuls tests. High and low groups have been indicated, respectively, by cross-hatching and plain shading. If an intermediate group exists it is shown by simple hatching. Diagram *a* shows three non-overlapping groups; the absence of overlap is indicated by barbed lines. Where two of the groups overlap only one barbed line is shown (diagram *b*). In diagram *c* the high and the low level both overlap the intermediate group. When more than one intermediate group exists, the intermediate groups are shaded together by means of simple hatching after the end groups have been defined as shown in diagram *d*. If the two end groups are contiguous (diagram *e*) the intermediate shading is omitted. When only two non-overlapping groups exist without any intermediate group a barbed line is drawn to indicate the non-overlap (diagram *f*). In diagrams *g* and *h* where the lower and higher groups overlap, it was decided to indicate the area of overlap as an intermediate group. Finally in diagram *i* no differentiation occurs; such maps have been arbitrarily shaded as a low group.

FIGURE 3.—Geographic distribution map of means of the character "forewing length" for the 23 localities of the study. The means have been transformed into probits and multiplied by 10 for ease of comparison. The outlines of the area have been explained in Figure 1. Shading of the area is as per Figure 2. The results of the SNK test are given in diagrammatic form in the right lower corner of the figure.

FIGURES 1-3

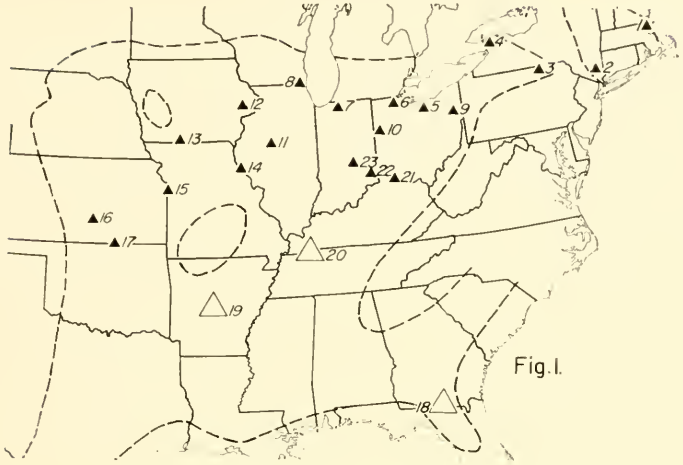

Fig.1.

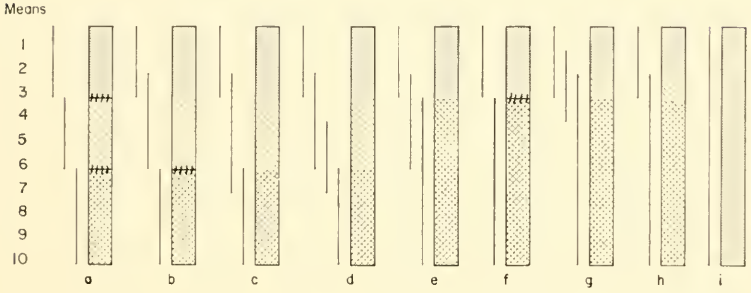

Fig.2.

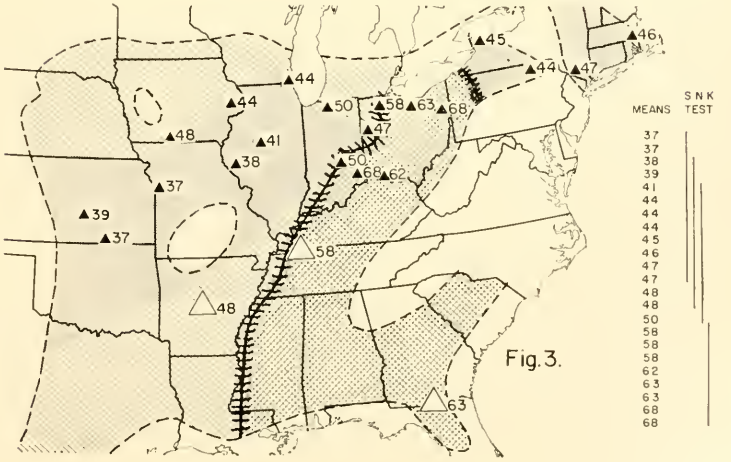

Fig.3.

FIGURES 4-6

FIGURE 4.—Geographic distribution map of means of the character "head length" for the 23 localities of the study. Explanation as in Figure 3.

FIGURE 5.—Geographic distribution map of means of character "head width" for the 23 localities of the study. Explanation as in Figure 3.

FIGURE 6.—Geographic distribution map of means of the character "thorax length" for the 23 localities of the study. Explanation as in Figure 3.

FIGURES 4-6

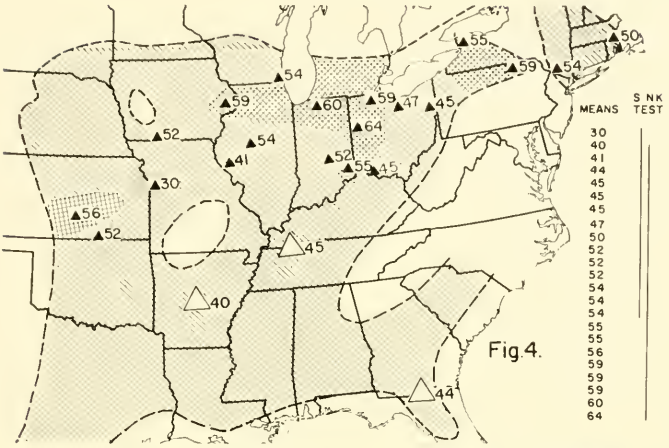
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Fig.4.

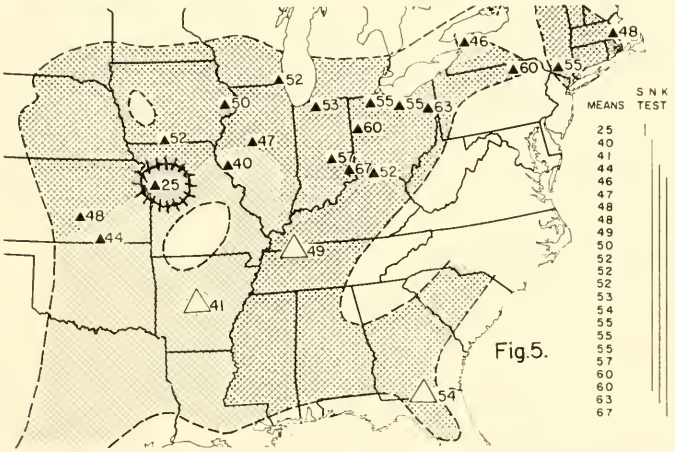
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Fig.5.

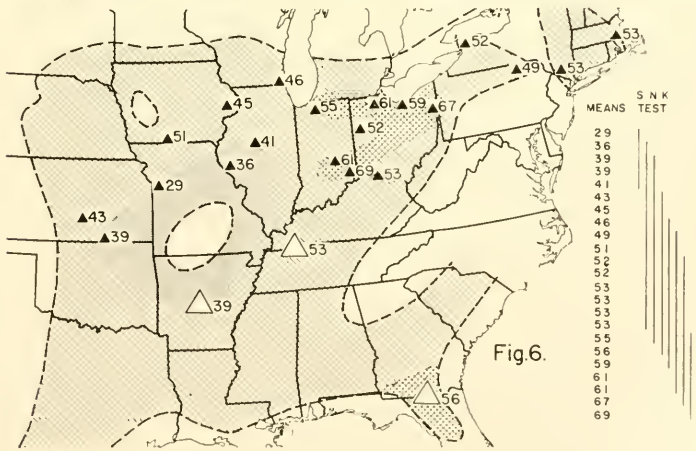
MEANS S N K TEST
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Fig.6.

FIGURES 7-9

FIGURE 7.—Geographic distribution map of means of the character "thorax width" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 8.—Geographic distribution map of means of the character "femur length" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 9.—Geographic distribution map of means of the character "tibia length" for the 23 localities of the study. Explanation as in Figure 3.

FIGURES 7-9

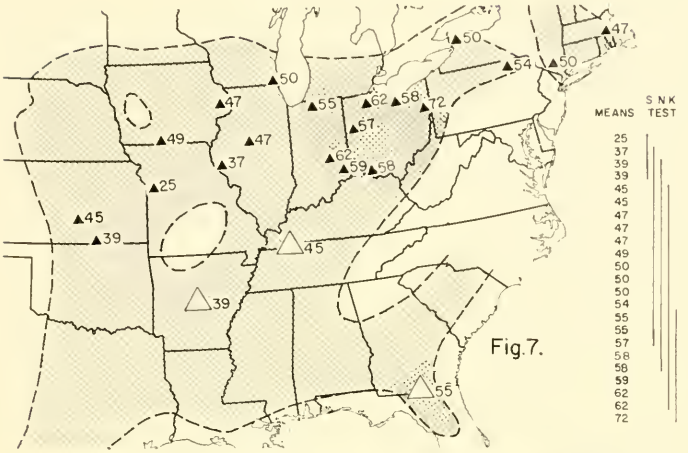


Fig.7.

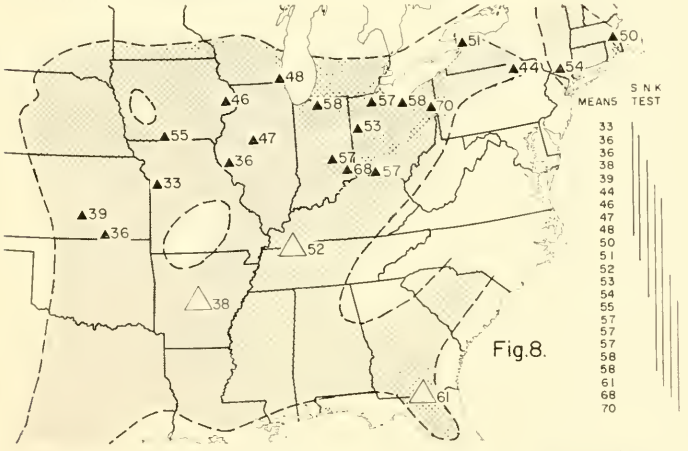


Fig.8.

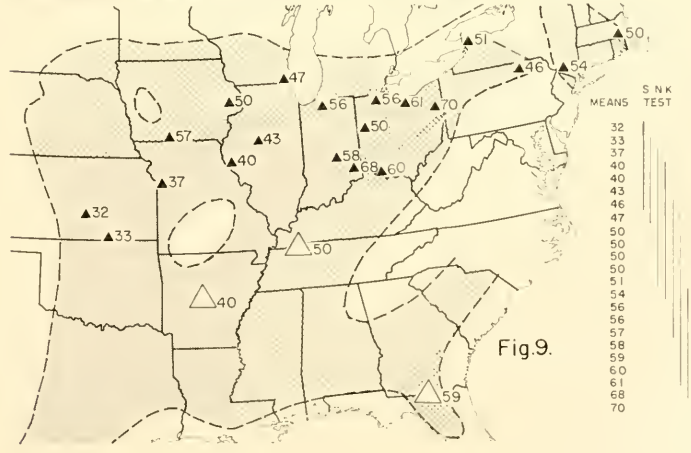


Fig.9.

FIGURES 10-12

FIGURE 10.—Geographic distribution map of means of the character "tarsus length" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 11.—Geographic distribution map of means of the character "antennal segment III length" for the 23 localities of the study. Explanation as in Figure 3.

FIGURE 12.—Geographic distribution map of means of the character "antennal segment IV length" for the 23 localities of the study. Explanations as in Figure 3.

FIGURES 10-12

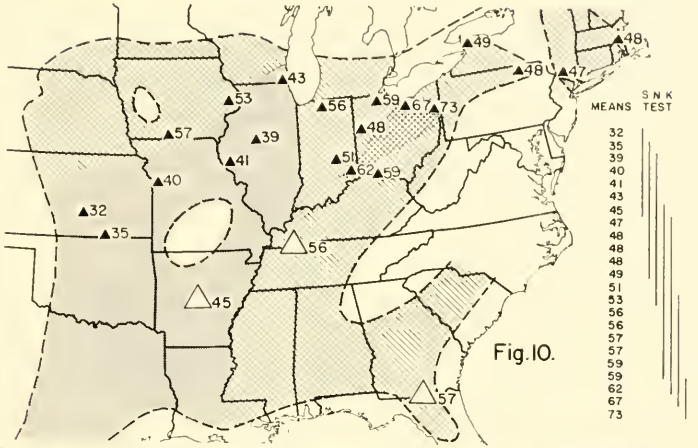


Fig. 10.

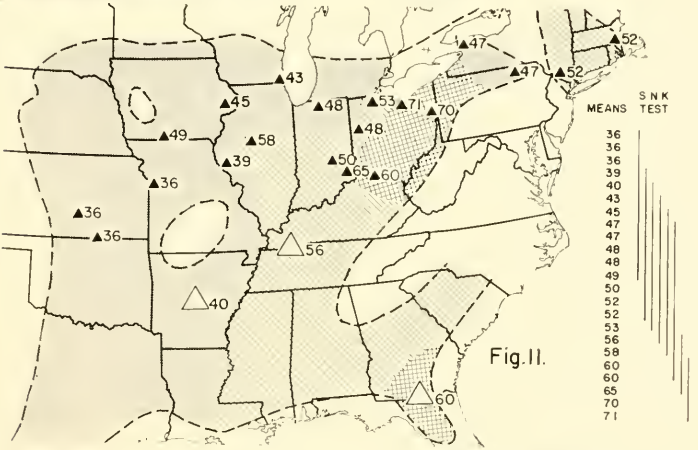


Fig. 11.

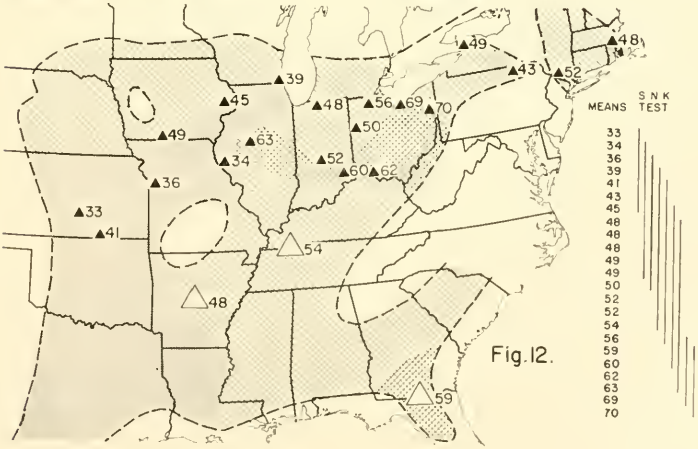


Fig. 12.

FIGURES 13-15

FIGURE 13.—Geographic distribution map of means of the character "antennal segment V length" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 14.—Geographic distribution map of means of the character "antennal segment VI length" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 15.—Geographic distribution map of means of the character "number of sensoria on antennal segment III" for the 23 localities of the study. Explanations as in Figure 3.

FIGURES 13-15

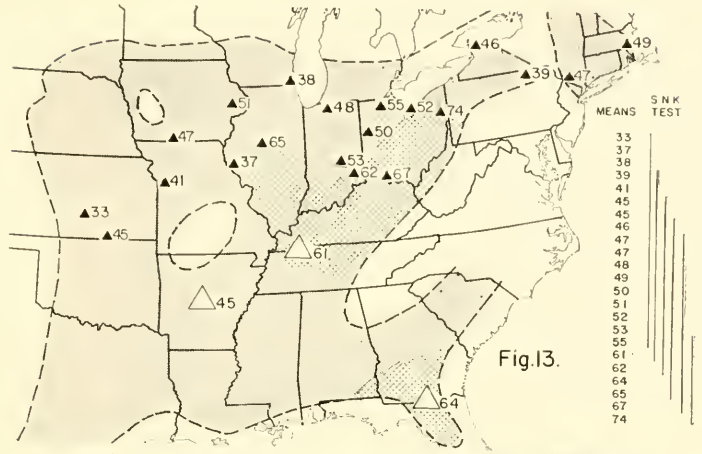


Fig.13.

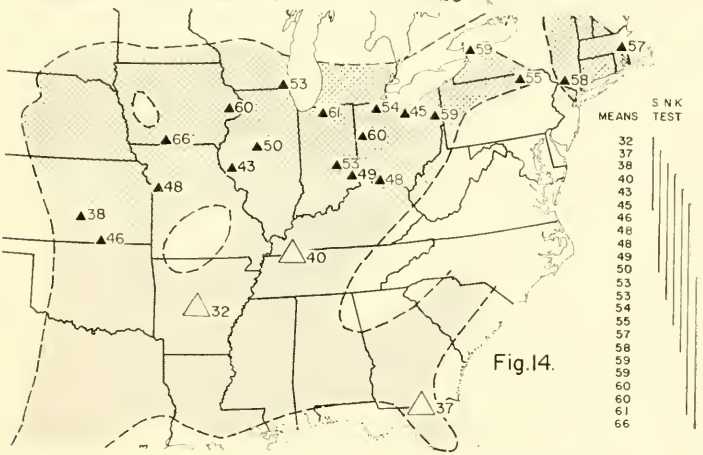


Fig.14.

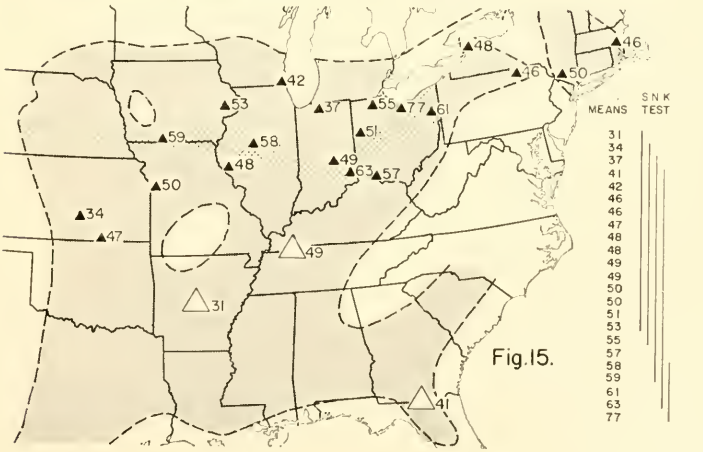


Fig.15.

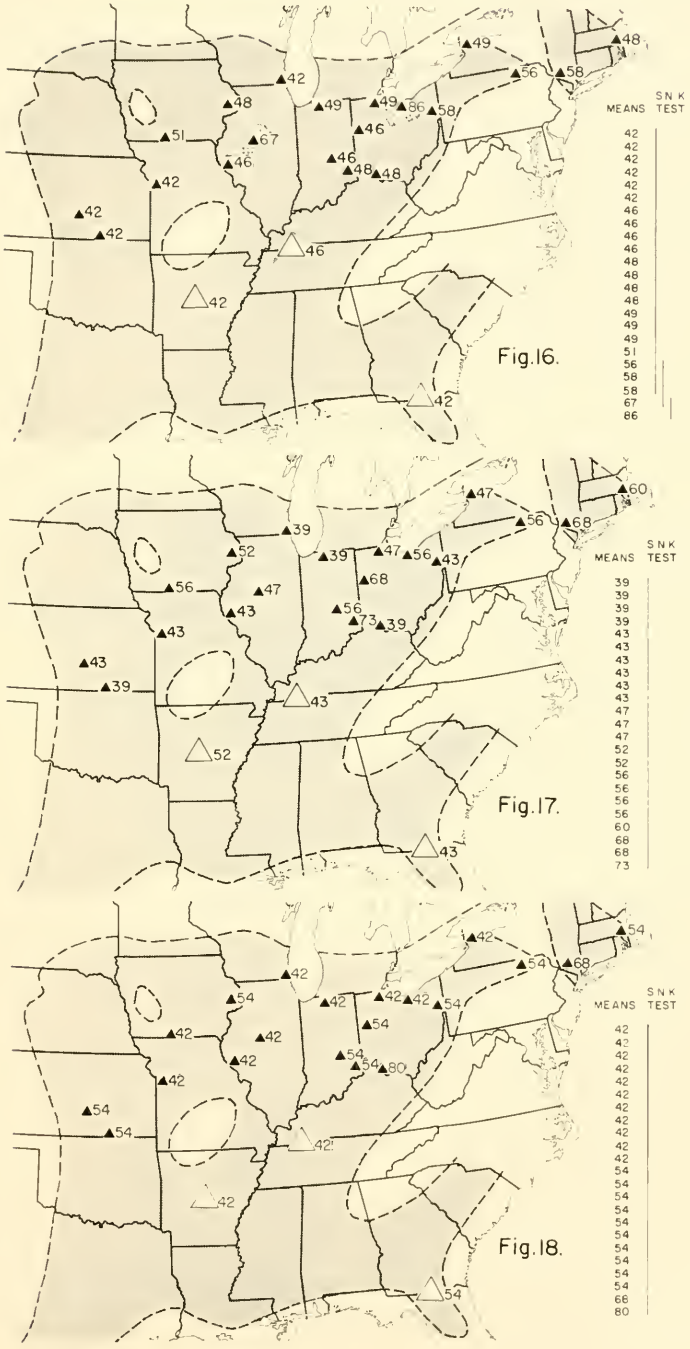
FIGURES 16-18

FIGURE 16.—Geographic distribution map of means of the character "number of sensoria on antennal segment IV" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 17.—Geographic distribution map of means of the character "number of sensoria on antennal segment V" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 18.—Geographic distribution map of means of the character "number of sensoria on antennal segment VI" for the 23 localities of the study. Explanations as in Figure 3.

FIGURES 16-18



FIGURES 19-21

FIGURE 19.—Geographic distribution map of means of the character "number of sclerotic islands in primary sensorium of antennal segment V" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 20.—Geographic distribution map of means of the character "number of sclerotic islands in the primary sensorium of antennal segment VI" for the 23 localities of the study. Explanations as in Figure 3.

FIGURE 21.—Geographic variation of factor I based on averages of characters "number of sensoria on antennal segment III," "number of sensoria on antennal segment IV" and "number of sclerotic islands in primary sensorium of antennal segment V." Explanations as in Figure 3.

FIGURES 19-21

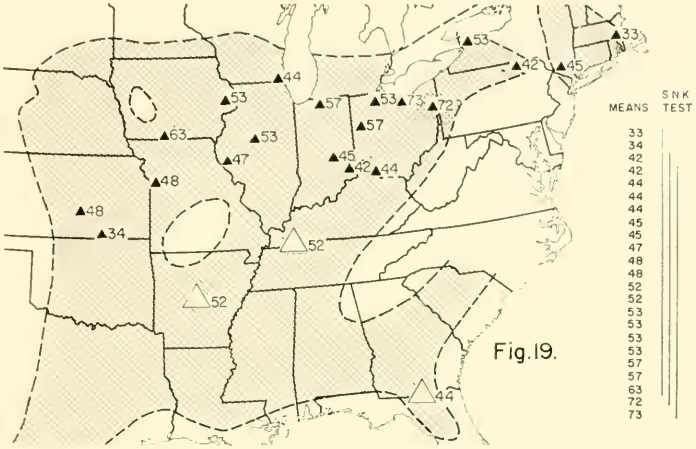


Fig. 19.

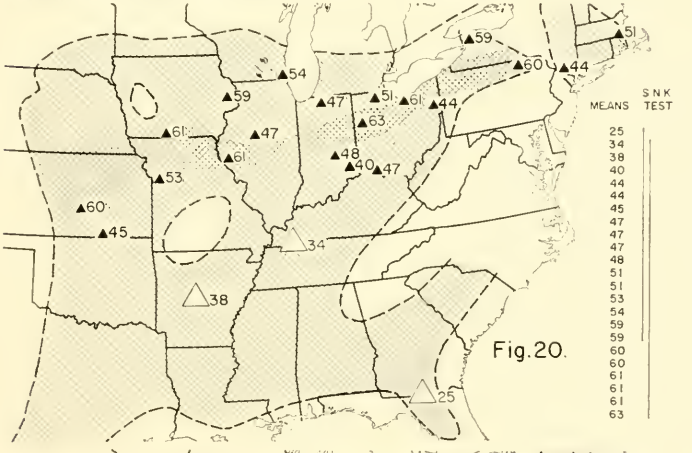


Fig. 20.

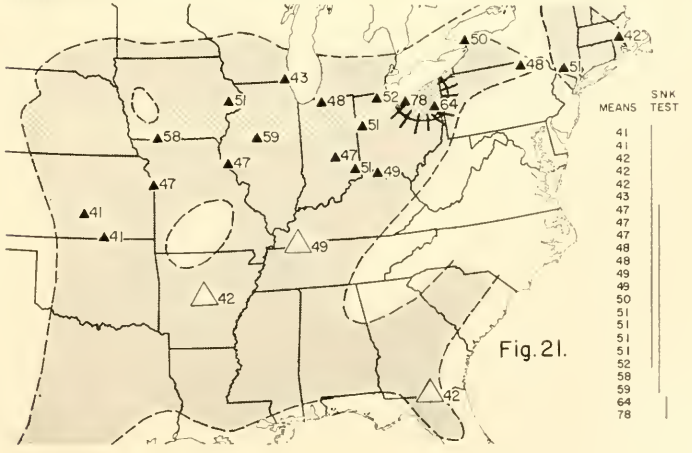


Fig. 21.

FIGURES 22-24

FIGURE 22.—Geographic variation of factor II based on averages of characters "head length," "head width" and "antennal segment VI length." Explanations as in Figure 3.

FIGURE 23.—Geographic variation of factor III representing average of characters "forewing length," "tibia length" and "tarsus length." Explanations as in Figure 3.

FIGURE 24.—Attempt to categorize distinct infraspecific populations on the basis of the three factors shown in Figures 21, 22 and 23. Symbols identifying the infraspecific populations are indications of the magnitude of each factor for a particular locality, *i* indicating the lowest level, 1 the intermediate level, and *I* the highest level. Thus a locality labeled *i,II,*111 indicates that this locality is in the low group as regards factor I, in the high group as regards factor II, and in the intermediate group as regards factor III. While we cannot make absolute statements about significance, it is generally safe to assume that the low and the high group are significantly different from each other. The different kinds of infraspecific populations are identified through 9 different shadings. The shadings were arbitrarily chosen and have no special significance.

FIGURES 22-24

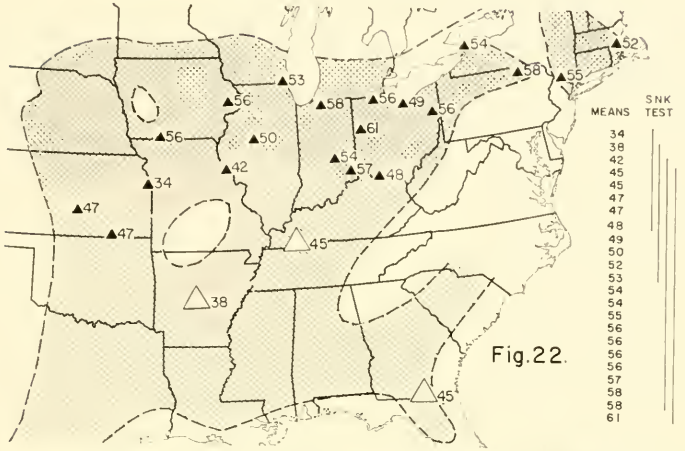


Fig. 22.

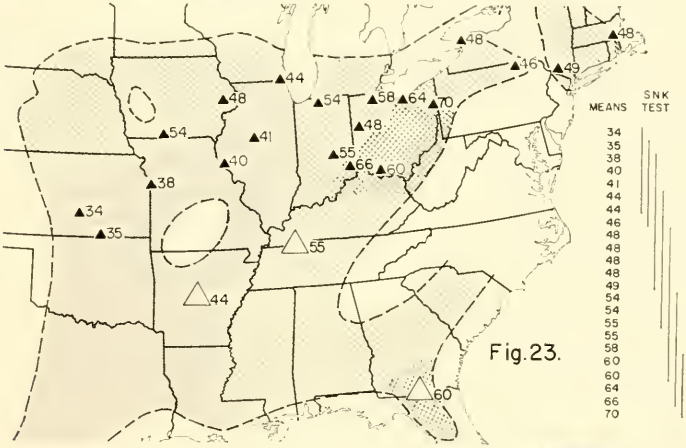


Fig. 23.

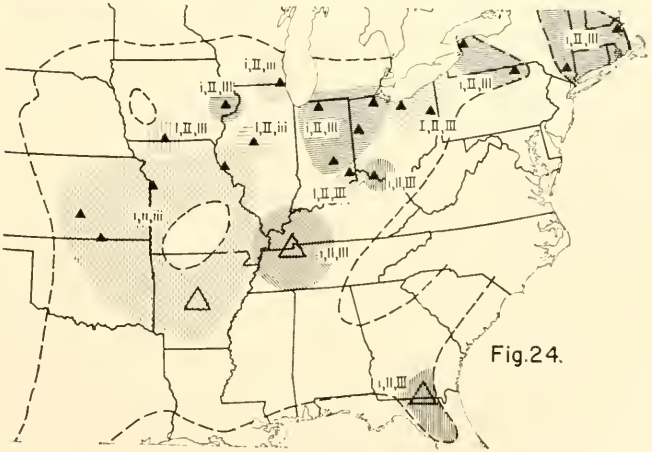


Fig. 24.

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Evolution of the Thoracic Musculature in Insects *

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ABSTRACT: Homologies of major thoracic muscles throughout the orders of insects are studied. It has been found that a major evolutionary tendency of the thoracic musculature has been along the line of reduction of certain muscles. All dorsal longitudinal muscles stretching out between neighboring segments in *Lepisma* have become lost with the development of the intersegmental phragmata in the Pterygota. The remaining three sets of the intrasegmental dorsal longitudinal muscles function as the indirect flight muscles in the Pterygota. The dorsal longitudinal muscles, in turn, have had a tendency to proliferate in size and become secondarily split in higher pterygote orders. One of the posterior tergo-coxal muscles seen in *Lepisma* has become the subalar-coxal (meral) muscle in position and function as a direct flight muscle in the Pterygota. Two tergo-anapleural muscles seen in *Lepisma* function as the indirect flight muscles in the Pterygota. The basalar-preepisternal, -trochantinal, and -coxal muscles in the Pterygota presumably have been derived from the anterior tergo-katapleural muscles seen in *Lepisma*. The thoracic muscles in Odonata and Ephemeroptera presumably have been derived from those in the non *Lepisma*-like ancestor.

The question as to how insects have acquired their ability to fly, and how their walking ability has changed with acquisition of wings has never been seriously considered in terms of the evolutionary change of the associated musculature. In this paper, an attempt is made to clarify some of these problems and the evolution of some other major thoracic muscles in a series of orders ranging from the Apterygota to the Pterygota.

It is generally believed in insect morphology that the thysanuran insects possess many ancestral patterns of structures from which those of the Pterygota have been derived. This was substantiated to a large extent, for the thoracic spina-sternal muscles in insects, in a recent study by Chadwick (1959). It can be expected, therefore, that the Thysanura would have retained the primitive patterns of the other thoracic muscles from which we might be able to trace

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the evolution of these muscles in other insects. The highly reliable studies on the thoracic musculature in *Lepisma saccharina* L. by Barlet (1953, 1954) are, therefore, repeatedly cited in this work as a basis for comparison and homology. His papers were preceded by a series of careful studies of the external and endoskeletal structures of the thorax in various groups of the Apterygota by Carpentier and Barlet himself. Many works on the thoracic musculature in pterygote insects, including Maki's (1938) monumental one dealing with forty-seven species of insects, have been published in the past few decades. Consequently, the data available for comparison can now be said to be sufficient.

It can be surmised that certain muscles, with the acquisition of the wings and some new structures associated with the flight mechanism, have changed their positions. In homologizing muscles, therefore, consideration is given to the possibility of a shift, within a certain limit, of the points of attachment of some muscles. This can be done with a reasonable assurance, especially when one end of a muscle is attached ventrally to a certain well-fixed structure, such as the coxal base, or the trochanter, etc.

Evidently in evolution, certain muscles have become secondarily split into two or more muscle fibers which may be more or less independent. The split is observed in the fibrillar muscles which occur commonly in flight muscles. It is known that a giant fiber in the fibrillar-type muscle is often cleaved into almost separate bundles of fibers by an intramuscular tracheal net. Partmann (1948), for instance, clearly showed that these giant fibers in the dorsal longitudinal muscles in various species of the Diptera are loosely adherent to each other in varying degrees, and this has eventually resulted, during the phylogeny of the Diptera, in a different muscle count for various groups of flies.

A much more dominant evolutionary tendency of the thoracic musculature, however, has been along the line of reduction in the number of muscles due to loss and possibly to fusion of certain muscles. In fact, when the muscles of *Lepisma saccharina* are compared with those of such primitive pterygote insects, as *Periplaneta* and *Corydalus*, the evolution of the musculature can be accounted for almost solely by the loss of certain muscles in these pterygote insects as will be shown below. The increase in the number of muscles, which is characteristic of certain muscle groups in higher pterygote orders, is evidently a secondary trend in the evolution of musculature. This is analogous to the production of certain elab-

orate external structures in higher insects. As will be concluded at the end of this paper, the thoracic musculature in the Odonata and the Ephemeroptera is apparently not derived from that of *Lepisma*. The musculature in these orders, especially that of the Odonata, often will be merely described or the homologies of muscles will only be suggested.

It is highly improbable that the production of entirely new muscles without any antecedent has taken place during evolution. This concept is, therefore, rejected in tracing the evolution of the musculature in the following discussion. The present discussion of the musculature pertains to the mesothorax unless otherwise noted. The terminology of the external pleural region is based on the one proposed and used by the author (1960, 1963). Figure 6 showing the primitive pattern of the pleural region of the pterothorax will be of help in following the discussion below. Chadwick (1959) already has summarized the knowledge of the spina-sternal muscles, so that these muscles are dismissed in the following discussion except for the sterno-coxal muscles.

Tergo-coxal and subalar-coxal muscles

(Figs. 3, 5A-C)

In *Lepisma* (Barlet 1954) there are three tergo-coxal muscles which arise dorsally from the posterior region of the tergum and are inserted on the posterior margin of the coxa (136, 137, 138, tergal remotors of the coxa). Two anterior tergo-coxal muscles are attached ventrally on the dorsal margin of the coxa (134, 135, probably tergal abductors of the coxa). In the prothorax of the same species, there are also three pairs of the posterior tergo-coxal muscles (131, 132, 133) which are homologous to muscles 136, 137, 138 in the mesothorax. One of them, which is homologous to muscle 136, can be regarded as consisting of two bundles of muscle fibers (*fide* Barlet). In *Lepisma*, therefore, there are three or possibly four posterior tergo-coxal muscles.

The maximum number of the tergo-coxal muscles known in the Pterygota is three, but this number can be reduced to two depending on the way they are counted. In *Corydalus cornutus*, for instance, Kelsey (1957) recorded two but says one of them (muscle 159) can be subdivided into two bundles of muscle fibers. Carbonell (1947) recorded three tergal remotors of the coxa (tergo-meral) in *Periplaneta americana*, but one of them can best be regarded as the tergal abductor of the coxa (anterior tergo-coxal muscle), not

homologous to any one of the three posterior tergo-coxal muscles in *Lepisma*. In a great majority of pterygote insects the posterior tergo-coxal (meral) muscles are represented either by two or by one muscle. It can thus be said that there is at least one less posterior tergo-coxal muscle in the Pterygota than in *Lepisma*.

In the Pterygota, however, there is the subalare above the epimeron and usually one muscle * extends between the subalare and the coxa or the meron which functions as a direct flight muscle. If this subalare-coxal (meral) muscle was originally one of the three posterior tergo-coxal muscles, there would be no difference in number of muscles under consideration between *Lepisma* and some of the more primitive pterygotes. Maki (1938) made, though inadvertently, an important observation in connection with this problem. He found in *Locusta migratoria manilensis* and in *Leucophaea surinamensis* that the subalar-coxal muscle is attached dorsally to the lateral area of the tergum in the late embryo, the muscle then becomes attached to the ventral base of the wing bud in the young nymph, and at the final stage of development this area becomes isolated as the subalare due to the membranization of the surrounding area. The subalare in the Pterygota thus can be regarded as a part of the tergum or the laterotergite, not a pleural structure as is generally believed, and the subalar-coxal (or meral) muscle is evidently homodynamous with one of three or four posterior tergo-coxal muscles in *Lepisma*.

If Maki's observation that the subalar-coxal (meral) muscle is homodynamous with a tergo-coxal muscle were correct we should expect the presence of one more posterior tergo-coxal muscles in the prothorax, in which the subalare does not occur, than in the pterothorax. It has been found by surveying the literature including Maki's that this is true in a majority of cases, although in some cases there are as many posterior tergo-coxal muscles in the pterothorax as in the prothorax. Exceptions to this tendency were found only in the Diptera (Maki 1938, Bonhag 1949) in which the tergal remotor of the coxa is absent in the prothorax and one tergal remotor of the coxa is present in the mesothorax.

Larsén (1945a) found that the meron is a secondary development in the Pterygota which occurred in direct association with the development of wings. The subalar-meral (coxal) muscle, which was primitively a remotor of the coxa, functions as a direct flight

* Matsuda (1956a), in *Blattella germanica*, found three subalar-meral muscles and says that they are superimposed on each other. They could have been regarded as a single muscle loosely subdivided. Carbonell (1947) regarded them as one in *Periplaneta americana*.

muscle in the Pterygota. The posterior tergo-coxal muscles in the Pterygota are attached either to the meron or to the basicosta of the coxa or both, and when these muscles are attached to the meron, they function primarily as indirect flight muscles (Larsén 1948). In certain orders (*e. g.*, some Orthoptera, Heteroptera, Dermaptera) the meron is not formed and all the muscles discussed here are attached to the posterior coxal rim. In the Diptera, the meron is transposed to the pleural wall and the tergo-meral muscles become the tergal depressor (Bonhag 1949).

The posterior tergo-coxal muscles have reduced their number to one in Mecoptera (Maki 1938, Hasken 1939), Trichoptera (Maki 1938), some Lepidoptera (Weber 1928, Maki 1938, Nüesch 1953), Heteroptera (Larsén 1945c) and some Diptera (Maki 1938, Larsén 1948, Bonhag 1949 etc.), or have become completely lost in Hymenoptera (Weber 1927, Maki 1938, Snodgrass 1942).

While the subalar-coxal (or meral) muscle is represented by a single pair of muscles in a great majority of pterygote insects, there are groups in which two pairs of the subalar-coxal muscles occur. In the Lepidoptera, for instance, Weber (1928) found two in *Papilio* and Nüesch (1953) found two in *Telea*. In both cases the presence of two pairs of muscles is due probably to a secondary split, since they are very thick. In *Amphigerontia* (Psocoptera) Larsén (1945b) recorded two subalar-coxal muscles. In the Ephemeroptera there are three dorsoventral muscles arising from the subalare. One thick muscle is attached ventrally to the furcasternum, a narrow one to the furca, and one on the coxal margin. In the absence of the well-developed meron, they appear to have become attached to the two different regions of the sternum (Knox 1935). If the postulation concerning the origin of the subalare by the separation from the tergum as described above is correct, then it would be possible in certain groups of pterygote insects that more than one posterior tergo-coxal muscles could remain attached to the subalare. In the Odonata, Asahina (1954) described a muscle between the coxa and the axillary plate and suggested that this was homologous to the subalar-coxal muscle. However, this may well be the homologue of one of the posterior tergo-coxal muscles. In either case, as the subalare is tergal in origin, the interpretation in favor of either one or the other is not too important. This is the only muscle in the pterothorax of the Odonata which can be homologized with the muscles under consideration. In the prothorax, however, Asahina's muscle 14 is probably homologous to

the posterior tergo-coxal muscle. In some Dipterans the subalar-coxal muscle has become lost (Smart 1959).

The question next arises as to what is the evolutionary fate of the two other tergo-coxal muscles (134, 135). Evidently, at least one of these muscles (135) has been retained in some pterygote insects, especially in the prothorax. According to Maki (1938) one or two of them are present in the prothorax of the Blattaria, Mantodea, Phasmoidea, Dermaptera, Plecoptera, Isoptera, Ephemeroptera, Thysanoptera and Hemiptera. Asahina's (1954) muscle 13 occurring in the prothorax is probably homologous with the muscle in question. These muscles are considered to be the tergal abductors of the coxa, always arising from the anterior region of the tergum and are inserted on the dorsal anterior margin of the coxa. One of the tergal abductors (134) in *Lepisma*, which is inserted on the posterior dorsal margin of the coxa in the Pterygota, has either become lost or has shifted its ventral point of attachment to the anterior dorsal rim of the coxa in the Pterygota. Although the tergal abductor of the coxa is nearly always represented by a single muscle, it is represented by two in Ephemeroptera and by three in Thysanoptera (Maki 1938). In the pterothorax Maki (1938) found a tergal abductor of the coxa only in the Coleoptera and *Locusta* of Orthoptera.

Tergo-trochantinal muscles

(FIG. 3)

In *Lepisma* there are four tergo-trochantinal muscles (149, 150, 151, 152). Three of them (149-151) arise from the anterior half of the tergum and are ventrally attached to the apical portion of the trochantin; muscle 152 arises from near the posterior end of the tergum and is inserted near the posterior coxo-trochantinal articulation. Of the anterior group of the tergo-trochantinal muscles, the point of origin of muscle 149 is the most anterior arising from an endoskeletal apodeme (Pseudophragma of Barlet). This muscle is most probably homologous to muscle 121 arising from the phragma in *Periplaneta* (Carbonell 1947) although its point of insertion is on the basisternum. Matsuda (1956a) found the same muscle in the mesothorax of *Blattella*. He further found the homologue of this muscle attached to the trochantin in the metathorax of the same species, and postulated (p. 17) that the attachment of this muscle to the lateral portion of the basisternum in the mesothorax is secondary. This muscle has apparently become lost in other pterygote

insects. In *Periplaneta* there are three more tergo-trochantinal muscles (118, 119, 120 of Carbonell 1947), but one of them is the tergo-anapleural muscle which has shifted its ventral point of attachment to the trochantin, as will be discussed elsewhere in this paper. If the above interpretation is correct cockroaches possess all the tergo-trochantinal muscles present in *Lepisma*. Muscle 150 and 151 in *Lepisma* are most probably the homologues of the two scuto-trochantinal muscles found in *Corydalus* (Kelsey 1957).

These tergo-trochantinal muscles in pterygote insects have acquired the function of bringing about flight action in addition to their primary function as the promotors of the coxa. They also have shifted their ventral points of attachment to the anterior margin of the coxa or to the apodeme attached to the coxa in certain higher forms (some Lepidoptera, some Coleoptera, Ephemeroptera, etc.) in which the trochantin is lost. The reduction in number of the tergo-trochantinal (or coxal) muscles in evolution is obvious. This set of muscles is represented by only one pair in many groups. These muscles have become completely lost in the Diptera, some Hymenoptera and Odonata.

Muscle 152 of *Lepisma* has become lost in the Pterygota with the loss of the posterior trochantino-coxal articulation in the latter.

Muscles of the trochanter

(Figs. 3, 4)

Tergo-trochanteral muscle: This muscle (124) is known as the tergal depressor of the trochanter and was found in the three thoracic segments in *Lepisma*. It always arises from near the middle of the tergum, and has been found in many less specialized groups of insects. In the Diptera, however, Smart (1959) found that this muscle is absent in many primitive Nematocerous flies. He thinks that this is due probably to the fact that a strong jumping action at the commencement of flight is not necessary in these flies. This muscle is lacking also in Odonata, Thysanoptera and Hymenoptera.

Anapleuro-trochanteral muscle: In *Lepisma* this muscle (195) arises dorsally from the anapleural apodeme *p* at the anterodorsal surface of the anapleuron, a position where the basalare occurs in the Pterygota. Judging from their positions this muscle and the basalar-trochanteral muscle in the Pterygota are most probably homologous, and hence the apodeme *p* in *Lepisma* and the basalare in the Pterygota are probably homologous. The basalar-trochanteral muscle is retained in some less specialized orders, *e. g.*, Orthoptera,

Plecoptera, Blattaria, Neuroptera, Mecoptera, Isoptera, Embioptera, etc. (Maki 1938). Maki (1938) recognized two pairs of the basalar-trochanteral muscles in Blattidae, but this is probably an error. More recent studies of cockroaches (Carbonell 1947, Matsuda 1956a) indicate the presence of one pair of this muscle, as in *Lepisma* and other insects.

Katapleuro-trochanteral muscles: In *Lepisma* there are two muscles that belong to this category (193, 194). The one (193) arises from the katapleural apodeme *c*, which is fused with the anapleural counterpart p *; another muscle (194) arises from the anterodorsal angle of the katapleuron. What is called the pleural depressor of the trochanter in pterygote insects (Maki 1938) is most probably homologous to one of these muscles in *Lepisma*. The one definitely identified as being the katapleuro-trochanteral muscle is found in the Odonata (Asahina 1954) and in *Siphlonurus* of the Ephemeroptera (Matsuda 1956b). The katapleuro-trochanteral muscle in these orders is probably homologous to muscle 194 in *Lepisma*, judging from their both dorsal and ventral points of attachment. Maki (1938) noted the pleuro-trochanteral muscle arising from various parts of the pleuron, *e. g.* from the pleural arm (*Eurostis* and *Cicadella* of Homoptera, Isoptera), and one from the pleural ridge (*Sigara* of Heteroptera). These are probably the katapleuro-trochanteral muscles. Exact homologies of these muscles with either one of the two katapleuro-trochanteral muscles in *Lepisma* are too difficult to determine. The one Maki described as arising from the dorsal portion of the episternum is the derivative from the basalar-trochanteral muscle. It is interesting to note that there is a strong tendency toward one of two situations occurring, namely that when the basalar-trochanteral muscle (anepisterno-trochanteral) is present the katapleuro-trochanteral muscle is absent and vice versa. This is true of even such primitive pterygotes as *Corydalus* (Kelsey 1957) or *Periplaneta* (Carbonell 1947). Neither the basalar-trochanteral nor the katapleuro-trochanteral muscle is present in the Hymenoptera (Maki 1938).

Trochantino-trochanteral muscle: This muscle (122) in *Lepisma* has been lost in the Pterygota.

Sterno-trochanteral muscle: This muscle is represented by muscle 123 in *Lepisma*. It arises from the endosternum (homologous to the furcasternum in the Pterygota) and is inserted on the trochanteral apodeme. This muscle arises from various parts of

* In the prothorax of *Lepisma saccharina* *c* and *p* are distinct.

the furca or the sternal apophysis in pterygote insects, and has been found in practically all orders of insects including the Odonata. However, in all species of the Ephemeroptera that have been studied (Dürken 1909, Knox 1935, Grandi 1947, Matsuda 1956b) this muscle is absent.

Tergo-anapleural muscles

(Figs. 4, 5D-F)

Barlet (1954) found in *Lepisma* four muscles belonging to this category (177, 178, 179, 180). Three of them (177, 178, 179) extend from the anterior region of the tergum to the anterior region of the anapleuron, and one of them (180) extends obliquely between the posterolateral region of the tergum and the anapleural sclerite. In a large number of pterygote insects two of these anterior muscles (177, 178) have apparently remained in the same relative positions and have stretched out a little more ventrad to be attached on the preepisternum of the anapleuron. These muscles, which presumably functioned as the promotors of the primitive subcoxa, function as indirect flight muscles in pterygote insects. These muscles have been called the tergo-sternal muscles by many previous workers, but the actual points of attachment are the preepisternum at least in holometabolous insects. The basisternum in holometabolus insects is more or less completely invaginated to form a median longitudinal ridge. It is lateral to this invaginated basisternum on which the so-called dorsoventral indirect flight muscles are attached. Kelsey (1957) also says "It is clear that no muscle, in any stage of development of the thorax of *Corydalus*, is inserted on any area considered truly sternal except for the furca and the spinasterna." Indeed, rarely is a muscle attached on the basisternum and then only on the marginal area, as Matsuda (1956a) contended.

Larsén (1948) refuted the idea that the indirect flight muscles (his tergo-sternal muscles) have been derived from the promotor muscles of the subcoxa on the ground that there is no muscle which corresponds to the indirect flight muscle either in the prothorax, or the mesothorax and metathorax in the Apterygota. Barlet's studies now convince us that there are such muscles. Another source of confusion probably stemmed from the fact that Larsén regarded, as many workers did at that time, the anapleural preepisternum as a part of the sternum. As Larsén (1948) says, however, the indirect flight muscles should not be considered as new structures. They existed in primitive insects as seen in *Lepisma*.

There is a strong indication that these primitively tergo-anapleural muscles have shifted their ventral points of attachment to neighboring structures due to a strong reduction of the preepisternum in some groups of the Pterygota. In Blattaria (fig. 5F), for instance, there is no tergal muscle which is attached to the reduced preepisternum, but there occur four tergo-trochantinal muscles in the metathorax of *Blattella germanica* (Matsuda 1956a). In other words, there is one more tergo-trochantinal muscle in *Blattella* than in *Lepisma*, or two more than in *Corydalus*. These facts strongly suggest that a tergo-preepisternal muscle has shifted its ventral point of attachment to the well-developed trochantin, accompanied by the reduction of the preepisternum. Another tergo-anapleural muscle in the cockroach has apparently become lost. The cockroach is specialized in these respects and the muscle transposed ventrally to the trochantin functions as an indirect flight muscle only secondarily.

In many forms of pterygotes, especially in holometabolous insects, the trochantin has become lost and the boundary between the anapleuron and the katapleuron also has become lost. In such cases the tergo-trochantinal muscles may become inserted on the uniformly sclerotized ventral region of the episternum. In Plecoptera (Grandi 1948, Wittig 1955) the tergo-anapleural muscle is very well developed and thick, and is secondarily attached to the definitive basisternum.* The muscle is composed of three bundles of muscle fibers in two rows (Wittig 1955), which arrangement is due most probably to a secondary split. A similar situation apparently occurs in some Lepidoptera (Weber 1928, Nüesch 1953), although Ehrlich and Davidson (1961) recognized two in *Danaus* (Lepidoptera). In Coleoptera, in which the forewing is not functional, the muscles in question have become completely lost in some species (Maki 1938). In Heteroptera, in which the boundary between the pleuron and the sternum is lost, the muscles are attached to the definitive sternum. According to Larsén (1945c) the muscle is absent in the pro- and metathorax in Heteroptera.

Evolutionary consequences of the muscles 179 and 180 in *Lepisma* will be discussed elsewhere.

* In the larva this muscle is the tergo-preepisternal (precoxale) muscle and is thin. The boundary between the preepisternum and the basisternum disappears when the insect develops into the adult (Wittig 1955).

Origin and evolution of the anapleuro-trochantinal, anapleuro-coxal and anapleuro-preepisternal muscles

(Figs. 4, 5A-C)

In *Lepisma* as well as in other apterygotes studied (Diplura and Collembola by Maki 1938, Thysanura by Barlet 1946, Thysanura by Tiegs 1955) there is no muscle which originates from the anterodorsal region of the anapleuron (basalare) and is inserted either on the ventral region of the anapleuron, or on the coxal margin, or on the trochantin. In the Pterygota, however, there are usually two or three muscles which arise from the basalare or the dorsal region of the anepisternum to insert on the above-mentioned ventral areas of the pterothorax. The question immediately arises as to just where these muscles in the Pterygota came from. If these muscles were derived from certain muscles in a *Lepisma*-like ancestor, we are compelled to suppose that there has been a shift of the dorsal points of attachment of certain anterior dorsoventral muscles found in *Lepisma* to the basalare in the Pterygota, which would be a similar condition to that found in the subalar region where a posterior tergo-coxal muscle or muscles evidently shifted their dorsal points of attachment to the subalare.

It appears to require a stretch of the imagination to conceive this idea, but this possibility is not unrealistic as it may sound. The basalare in cockroaches, for instance, becomes recognizable only at the final stage of development by an increased degree of pigmentation, and the anepisternum including the basalare area (anterior dorsal region of the anapleuron) is deeply invaginated and attached to the inner wall of the tergum. It is not difficult at all to visualize, under such circumstances, that some tergal muscles became transferred to the basalare or to the dorsal margin of the anepisternum. As Barlet (1950) has shown, the anapleural area in the Thysanura is largely membranous, and the anapleural tendon (homologous to the basalare in the Pterygota) is relatively small, so that the dorsal anapleural area simply cannot serve as dorsal points of attachment of these three muscles. With increased sclerotization of the anapleuron in the Pterygota, however, some tergal muscles could have shifted their points of attachment to the basalare or to the dorsal area of the anepisternum. In any case, the production of three (as will be discussed below) entirely new muscles without any ante-

cedent in the pleuron is less than a possibility, and the shift of the dorsal points of attachment of the three muscles to the basalare here is at least more probable than the complete loss of all of them. If this postulation is accepted, we can, in fact, homologize all muscles but one * that are present between the tergum and the area below the dorsal margin of the episternum in *Lepisma* and those occurring in the corresponding position in some primitive pterygotes.

It may be argued further that if the tergo-pleural muscles have shifted their points of dorsal attachment to the basalare, there should be more tergo-pleural muscles in the prothorax, in which the basalare does not occur, than in the pterothorax. The part of the prothorax anterior to the coxa, however, is generally highly specialized, due to the presence of the cervical sclerites and to the reduction of the area itself. Consequently, the number of the muscles identifiable as the tergo-pleural muscles has been greatly reduced. The one Maki (1938) called "the ordinary tergo-pleural muscle" is probably homologous to a tergo-katapleural muscle, and is represented by one pair in most orders. Often there occurs no muscle arising from the pleuron at all in the prothorax which can be homologized with the three muscles under consideration. The comparison of the muscles between the prothorax and the pterothorax does not provide a basis for the argument in connection with the problem concerned here.

There are five tergo-katapleural muscles (160, 161, 162, 163, 164) in *Lepisma,* for which the evolutionary fates were not accounted for in the preceding discussion. Presumably three of these muscles have shifted their dorsal points of attachment from the tergum to the basalare with the acquisition of the wing, since in certain primitive pterygote insects (*e. g., Corydalus,* Kelsey 1957, *Agulla,* Matsuda 1956a) there are present the basalar-coxal, basalar-preepisternal, basalar-trochantinal muscles. As to what particular tergo-katapleural muscles have been transferred to the basalare we can only suggest. Presumably the anterior three of them (160, 161, 162) have undergone this shift, as they are located anteriorly on the tergum and their ventral points of attachment are much closer to the trochantin, to the coxa, and to the preepisternum than those of the posterior two muscles (163, 164). From these ventral points of attachment of the muscles 160, 161, 162, it is not difficult at all to suppose that they have become attached to the preepisternum, to the trochantin, and to the anterior coxal base, considering the

* Muscle 152, the loss of which was accompanied by the loss of the structure for attachment ventrally. See table 1.

fact that the katapleural area in the Pterygota is often much narrower ventrally than in *Lepisma*.

In cockroaches there are two anepisterno-trochantinal muscles (122, 123 of Carbonell 1947) * and one episterno-coxal muscle (126 of Carbonell 1947),** but one of the anepisterno-trochantinal muscles is most probably homologous to the basalar-preepisternal muscles. In Blattaria the preepisternal region, as noted previously, is so strongly reduced that the basalar (or anespisterno)-preepisternal muscle must have shifted its ventral point of attachment to the well-developed trochantin. In cockroaches the muscle, as a direct flight muscle, is probably of lesser importance than in other insects.

In holometabolous insects, on the contrary, the preepisternal region is well-developed and very often it becomes indistinguishably fused with the katepisternum and the trochantin also becomes lost, thereby forming a broad uniformly sclerotized area of the episternum. This is especially pronounced in Hymenoptera, Diptera and in the metathorax of Coleoptera. In many groups of holometabolous insects two basalar muscles are inserted on this highly sclerotized ventral area of the episternum. In such cases one of them is probably a derivative from the basalar-trochantinal muscle, and the basalar-coxal muscle must have become lost. In the mesothorax of Coleoptera the forewing is not functional, and these muscles have become lost except for the basalar-coxal muscle in a few species Maki (1938) studied. The loss of the muscles evidently occurred as a parallel event with the loss of the function of the forewing in this order. In the Heteroptera (Larsén 1945c) the basalar-definitive sternal muscle occurs only in the mesothorax in which the wing is functional. In the Odonata Asahina (1954) found two muscles arising from a cap tendon, which hangs from the membrane anterior to the humeral plate and is inserted on the preepisternum and the preepisternal tendon. He regards this cap tendon as the homologue of the basalare. If so, the muscle must be homologous to the basalar-preepisternal and the basalar-trochantinal muscles respectively. In the absence of the trochantin in the Odonata the latter is attached to the preepisternal area. Asahina (1954) further suggests a possibility that his muscle 26 stretching out between the coxa and the humeral plate is the homologue of the basalar-coxal muscle. In the Ephemeroptera there are two muscles connecting the basalare and the prothoracic furca (Knox 1935, Matsuda 1956b). Whether

* A short muscle (124 of Carbonell) is not considered here, as it is apparently not homologous to any one of the muscles under consideration.

** Misspelled as "sternal promotor of the coxa."

or not they are homologous to the muscles under consideration in other insects cannot be determined.

Katapleuro-coxal muscles

(FIG. 4)

There are two katapleuro-coxal muscles (191, 192) in *Lepisma*. Muscle 191 arises from within the katapleuron near the catapleural tendon and is inserted on the dorsal anterior margin of the coxa. This muscle is most probably homologous to the third pleural abductor of the coxa of the authors (Snodgrass 1929, Maki 1935, Albrecht 1954) in the Pterygota including the Ephemeroptera and Odonata. It always arises from the area just anterior to the pleural ridge and from the precoxal suture (or costa) in the Pterygota when it is present.

In *Lepisma* there is another muscle (192) which arises from the katapleural tendon c and is inserted on the ventral posterior margin of the coxa. In the Pterygota there is sometimes another pleural abductor, but it is attached to the coxal margin anterior to the point of attachment of the pleural abductor (homologue of 191). Muscle 192 in *Lepisma* and the latter pleural abductor of the coxa in the Pterygota probably function differently. Moreover, the point of origin of this muscle in the Pterygota varies in various species, arising often from the anapleural region. The homology of this muscle and muscle 192 in *Lepisma* is, therefore, open to question. Snodgrass (1929) in *Dissosteira* and Albrecht (1954) in *Locusta* described this muscle as being represented by two muscles, but they can be regarded as one muscle secondarily split, as they are inserted on the same place of the coxal margin and their points of origin are right next to each other along the secondary transverse internal ridge of the episternum. In *Megacrania* of Phasmoidea (Maki 1935) it was found that these subdivided muscles are also inserted on the same place, but their dorsal points of origin are quite far apart, one of them arising from the upper end of the episternum far from the wing base.

Sterno-coxal muscles

(FIG. 3)

In *Lepisma* there occur six endosterno-coxal muscles. The anterior spina-coxal muscles (106, 107) arise from the spina of the preceding segment. The former is inserted on the coxal process below the posterior coxo-trochantinal articulation, and the latter near the anterior tergo-trochantinal articulation (probably the promotor of

the coxa). Two muscles (108, 110*) arise from the endosternum; the former is attached to the median point of trochantino-coxal articulation and the latter on the coxal process arising from the dorsal posterior region of the coxal margin. Another muscle (109) arises from the basisternum just in front of the furcasternum and is inserted near the posterior end of the trochantin. The last muscle (111) arises from the region *m* which corresponds to the intersegmental spina between the mesothorax and metathorax, and is inserted on the posterior margin of the coxa. All together there are six coxal muscles arising from the endosternum in *Lepisma.* Superimposed on the more elaborate coxo-trochantinal articulations the six muscles in *Lepisma* must function in a somewhat different way from those in the Pterygota.

In the pterygota the posterior coxo-trochantinal articulation has become lost, and the median articulation is replaced by the pleuro-coxal articulation, accompanied by the development of the pleural ridge. The number of the endosterno-coxal muscles also have had a tendency to reduce in number. Yet it has been found that all muscles except one (106) in *Lepisma* are apparently retained in varying numbers in various groups of the Pterygota, although their positions have undergone some change.

Czihak (1953) found, in *Sialis* (Neuroptera), two spinal remotors arising from the first spina (intersegmental between the pro- and mesothorax). One of them is inserted on the hind region of the meron, and the other on the area behind the coxo-pleural articulation of the prothoracic leg. In *Lepisma* these apparently homologous muscles (104, 105)† arise from the area corresponding to the base of the furca (104) and from the spinal area (105). Their points of origin are therefore different from those in *Sialis,* although they are inserted on similar points along the coxal margin. The condition in *Sialis* could possibly be regarded as secondary. The homologues of muscles 107 and 111, are retained in some Orthoptera (Maki 1938). The presence of the homologue of muscle 106 in the Pterygota is not known with certainty. At least it has become lost in a great majority of pterygote insects.

In some hemimetabolous insects a sternal adductor (arising from the base of the furcal arm and having its insertion on the median basal rim of the coxa) is present. There are at least a promotor of the coxa extending between the furcal arm and the anterior rim

* Chadwick (1959) regarded this muscle as a spina-coxal muscle, but it arises from the region *b* of the endosternum which is anterior to the poststernite (see Carpentier 1946). The area *m* alone can be regarded as corresponding to the spinal area.

† Exactly homologous to muscles 110 and 111 in the mesothorax.

of the coxa, and a remotor between the furca and the posterior rim of the coxa in practically all pterygote insects that have been studied, and a muscle between the posterior region of the basisternum and the anterior point of coxal articulation in certain groups (*e. g.*, larva in Plecoptera, Wittig 1955). To what endosterno-coxal muscles of *Lepisma* (108, 109, 110) these muscles correspond cannot be said with certainty, as they are different in points of attachment from those of muscles 108-110 in *Lepisma*. The sterno-coxal muscles in holometabolous insects have apparently been greatly reduced in number. Often the sterno-coxal muscles are represented by the ordinary promotor and remotor arising from the furca alone. This is due probably to the close proximity of the two coxae to the median longitudinal axis, thereby restricting the movement of the coxa on the transverse axis of the body. In fact, in the larvae of certain holometabolous insects, in which the coxal bases are widely separated from each other, there are more sterno-coxal muscles (*e. g.*, *Corydalus*, Kelsey 1957; *Dytiscus*, Speyer 1922).

Dorsal longitudinal muscles

(FIG. 2)

Barlet (1953) described nineteen dorsal longitudinal muscles occurring in three thoracic segments in *Lepisma*, of which several stretch into the basal abdominal segments. Amazingly large numbers of muscles extend freely from one segment to another. For instance, four muscles (1, 5, 6, 7) extend between various parts of the protergum and various parts of the mesotergum, and three muscles (8, 9, 10) between various parts of the mesotergum and various parts of the metatergum including its posterior end. These muscles must undoubtedly give a high degree of flexibility in contracting the body lengthwise in *Lepisma*. This kind of muscular arrangement, however, has been completely relinquished in the Pterygota. All dorsal longitudinal muscles in the Pterygota are either intrasegmental or between the anterior part of the tergum and the phragma, or between phragmata.

It can be easily surmised that with the acquisition of the wing the intersegmental phragmata also have developed more or less strongly in the Pterygota to serve as the supports for the dorsal longitudinal muscles which now function as powerful indirect flight muscles. Further, with the development of the phragmata the muscles crossing the segmental borders have become mechanically impossible of functioning, resulting in their complete loss in the Pterygota. The remaining three dorsal longitudinal muscles (11,

12, 13) in *Lepisma* are, in fact, very similar in their positions to those in such a primitive pterygote insect as the cockroach. That is muscle 12 can be homologized with the median dorsal muscle, 11 and 13 with the lateral oblique muscle (lateral dorsal muscle) in the cockroach.

No tendency is noted for these muscles to have become reduced in number in higher pterygote insects. On the contrary, they have even generally proliferated in size and become secondarily split in varying degrees in various groups of most pterygote insects. Partmann's (1948) study on the dorsal longitudinal muscles in various species of the Diptera is too interesting and important to pass over in this connection. He found that the dorsal longitudinal muscles are each composed of more or less distinct large muscle fibers (which are now known as giant muscle fibers). He concluded that with the attainment of certain body size the muscles have undergone modification. The modification has been achieved by the decomposition of a muscle into more or less distinct bundles of giant fibers in Nematocera, and by the intramuscular invagination in Cyclorhaphous flies, and finally by a more advanced intramuscular invagination in certain muscles, combined with complete split of certain other muscles in *Eristalomyia* (Syrphidae). In generally more primitive Nematocerous flies he found three or four pairs of the dorsal longitudinal muscles, whereas in Cyclorhaphous flies a maximum of 12 pairs of them were found. In the Diptera at least, the increase in number of the dorsal longitudinal muscles in phylogeny has apparently been due primarily to the intramuscular invagination which eventually leads to complete split of a muscle. Partmann (1948) further showed that within the same group of flies (*e. g.*, within a genus) the muscles tend to become fused with each other, and often original individual muscles are not recognized or obscure.

The loss of the lateral dorsal muscles has occurred, however, in *Atractomorpha* (Orthoptera), Thysanoptera, some Hymenoptera and in some Coleoptera (Maki 1938). In the Odonata the lateral dorsal muscles alone are present.

Other muscles

(Figs. 2, 4)

In *Lepisma* there are three posterior tergo-sternal muscles (84, 85, 86). Muscle 84 stretches out between the median lateral region of the tergum and the furca; 85 between the anterolateral corner or the following segment (here the metatergum) and the furca; 86

between the anterolateral area of the tergum of the following segment behind muscle 85 and the furca. All of these muscles are apparently retained in varying numbers in various groups of pterygote insects.

Muscle 85 of *Lepisma* is most probably the homologue of what Maki (1938) called the ordinary posterior tergo-sternal muscle in many pterygote insects. This is located in the same relative position as in *Lepisma*. Sometimes the apparently homologous muscle arises from the phragma (Isoptera, Coleoptera, Maki 1938), and the muscle between phragma and the coxal margin in the Ephemeroptera (Matsuda 1956b) may possibly be the homologue of this muscle. This muscle is absent in the Odonata (Asahina 1954). Muscle 86 in *Lepisma* can be homologous with the muscle between the peritreme of the spiracle, or the sclerotized area surrounding the first spiracle and the furca in some insects (Mantodea, Embioptera, Hemiptera, Maki 1938). In *Lepisma*, at least in the metathorax, the spiracle is apparently intrasegmental. It is conceivable that the muscle arising from near the spiracle has shifted anteriorly with the shift forward of the spiracle to occupy an intersegmental position in the Pterygota, although Barlet (1953) does not mention the association of this muscle with the spiracle.

The first axillary sclerite (Maki 1938) or the second axillary sclerite (Matsuda 1956b)—mesofurcal muscle in the Ephemeroptera occupies a position very similar to muscle 84 in *Lepisma*, and this leads one to suspect that the former has been derived from the latter. In *Siphlonurus* of Ephemeroptera (Matsuda 1956b) there are two muscles of the second axillary sclerite arising from the precoxal costa on the episternum and from the sternal apophysis, and one muscle of the first axillary sclerite coming from the coxal process in the mesothorax. In the Odonata there are two prefurcatergal apophyseal or -scutal muscles. If these dorsoventral muscles were derived from the muscles in the apterous ancestor, the dorsoventral musculature in *Lepisma* is quite inadequate to account for their origin, as there is only one muscle (84) which could be ancestral to one of these muscles in the Ephemeroptera and Odonata. In *Lepismachilis* (Barlet 1946), however, there occur seven tergoendosternal muscles and they could be ancestral to the muscles in question, although Barlet attributed the presence of these muscles in *Lepismachilis* to the jumping action peculiar to them. In any case, the origin of the direct flight muscles at least in the Odonata should be sought for in non-*Lepisma*-like ancestor. As often noted

in the preceding discussion, the thoracic musculature in the Odonata and Ephemeroptera often conspicuously deviates from that of *Lepisma,* while many muscles in other primitive pterygote orders, such as the Blattaria or Neuroptera, can be directly homologized with those of *Lepisma.* As Lemche (1940) maintained the fossil evidence does not contradict the idea of the diphyletic origins of pterygote orders. Both groups, the Palaeoptera and the Neoptera, occurred at the same time from the lower Pennsylvanian onward. The origin of the thoracic musculature including those under consideration in Odonata and Ephemeroptera may better be considered separately.

There are several muscles which occur in the tergo-pleural region in *Lepisma,* the evolutionary fate of which was not accounted for in the preceding discussion. They are muscles 159, 163, 164 (tergo-katapleural) and 179, 180 (tergo-anapleural), most of which occupy the dorsal region of the pleuron and the tergum. The location of these muscles leads one to suspect strongly that they are homologous to certain muscles occurring in similar relative positions in many pterygotes (such as those between the anterolateral margin of the tergum and the anepisternum or the basalare, and those between various parts of the pleural ridge and the posterior lateral margin of the tergum), although the homologies of individual muscles cannot be attempted. It is also probable that the muscle or muscles of the axillary sclerites in the neopterous pterygote insects have been derived from these muscles found in *Lepisma.*

SUMMARY

1. A great majority of the thoracic muscles in *Lepisma* have been retained in primitive pterygote insects, such as the Blattaria or Megaloptera. The major evolutionary tendency of the thoracic musculature has been the loss of muscles.
2. All dorsal longitudinal muscles stretching out between neighboring segments in *Lepisma* have become lost with the development of the intersegmental phragmata in the Pterygota. The remaining three sets of the intrasegmental dorsal longitudinal muscles function as indirect flight muscles in the Pterygota.
3. The dorsal longitudinal muscles have had a tendency to proliferate in size and become secondarily split in higher pterygote orders.
4. One of the posterior tergo-coxal muscles in *Lepisma* has become the subalar-coxal (meral) in position to be a direct flight muscle in the Pterygota.

5. Two tergo-anapleural muscles in *Lepisma* function as the indirect dorsoventral indirect flight muscles in the Pterygota. They have stretched ventrad, proliferated in size and become secondarily split in certain orders.
6. The basalar-preepisternal, -trochantinal, and -coxal muscles in the Pterygota presumably have been derived from the anterior tergo-katapleural muscles found in *Lepisma*.
7. The thoracic muscles in Odonata and Ephemeraptera presumably have been derived from those in the non-*Lepisma*-like ancestor.
8. Homologies of muscles between *Lepisma* and pterygotes are summarized in table 1.

TABLE 1

Lepisma saccharina	Pterygotes
1, 5-10 (Dorsal longitudinal)	Lost.
11-13 (Dorsal longitudinal)	Median dorsal, lateral dorsal muscles. (Indirect flight muscles). Increased in number by split in higher orders.
84 (Posterior tergo-endosternal)	Muscle of second axillary sclerite in Ephemeroptera (?).
85 (Posterior tergo-endosternal)	Ordinary posterior tergo-sternal muscle in many orders.
86 (Posterior tergo-endosternal)	Near spiracle-furca muscle (?).
106 (Spina-coxal)	Lost.
107 (Spina-coxal)	Present in a few groups.
111 (Spina-coxal)	Present in a few groups.
108-110 (Endosterno-coxal)	At least two of them are present in many orders.
122 (Trochantino-trochanteral)	Lost.
123 (Endosterno-trochanteral)	Present in a great majority of pterygotes.
124 (Tergo-trochanteral)	Tergal depressor of coxa. Present in many orders.
134-135 (Anterior tergo-coxal)	Maximum 2 tergal abductors of the coxa in the prothorax. 1 in the pterothorax in some species.
136-138 (Posterior tergo-coxal)	2 posterior tergo-coxal (meral) and 1 subalar-coxal (or meral) muscle.
149-151 (Anterior tergo-trochantinal)	3 anterior tergo-trochantinal in Blattaria; 149 lost in other insects; represented by one in many species.
152 (Posterior tergo-trochantinal)	Lost with the loss of the posterior trochantino-coxal articulation.
159 (Posterior tergo-katapleural)	Probably became a muscle between the tergum and the dorsal part of the pleuron, or lost.
160-162 (Anterior tergo-anapleural)	Presumably have become basalar-preepisternal, -trochantinal, -coxal muscles.

TABLE I—Concluded

Lepisma saccharina	Pterygotes
163-164 (Anterior tergo-anapleural)	Probably have become muscles between the tergum and dorsal region of the pleuron.
177-178 (Anterior tergo-anapleural)	Have become tergo-preepisternal (or definitive sternal) muscles which function as indirect flight muscles.
179-180 (Median and posterior tergo-anapleural)	Probably have become the muscles between the posterior region of the tergum and the pleuron.
191 (Anterior katapleuro-coxal)	Third pleural abductor of the coxa in many groups.
192 (Posterior katapleuro-coxal)	First and second pleural abductors of the coxa (?).
193-194 (Katapleuro-trochanteral)	One of them exists in many species.
195 (Anapleuro-trochanteral)	Basalar-trochanteral muscle. Retained in less specialized orders.

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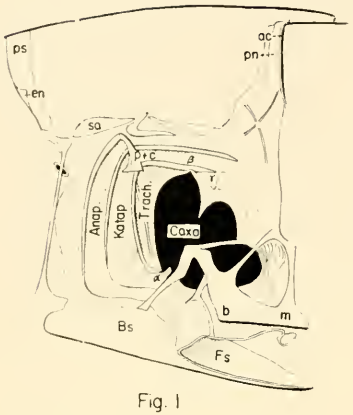

Fig. 1

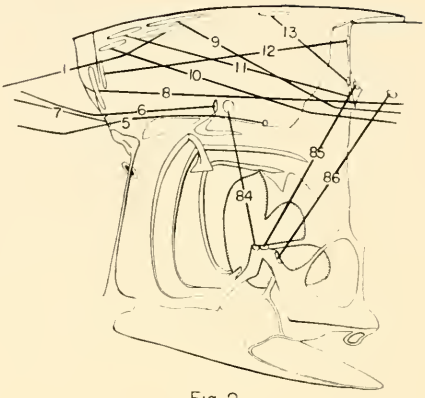

Fig. 2

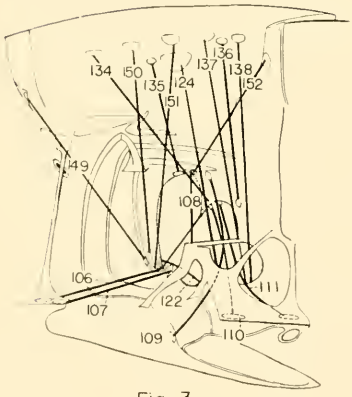

Fig. 3

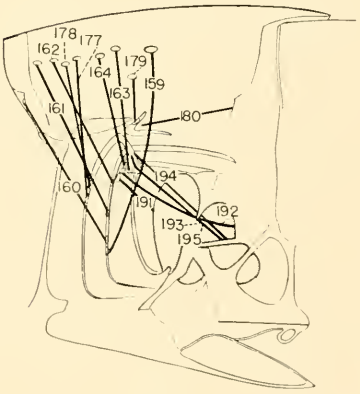

Fig. 4

FIG. 1.—Sagittal section of the mesothorax in *Lepisma saccharina* L. Bs.: Basisternum; Fs.: Furcasternum; m: spinal area; b: furcal area; Anap.: Anapleuron; Katap.: Katapleuron; Troch.: Trochantin; sa.: Anapleural sclerite; Ps.: Prescutum; en.: endonotal lamella (Pseudophragma); ac.: Antecosta; pn.: Postnotum; α: Anterior trochantino-coxal articulation; β: Median trochantino-coxal articulation; γ: Posterior trochantino-coxal articulation; p + c: Apodemes of ana- and katapleurons, p and c are separated in the prothorax. (From Barlet 1951.)

FIG. 2.—Mesothoracic muscles in *Lepisma saccharina* L. (Barlet 1953.)

FIGS. 3 and 4.—Mesothoracic muscles in *Lepisma saccharina* L. (Barlet 1954.)

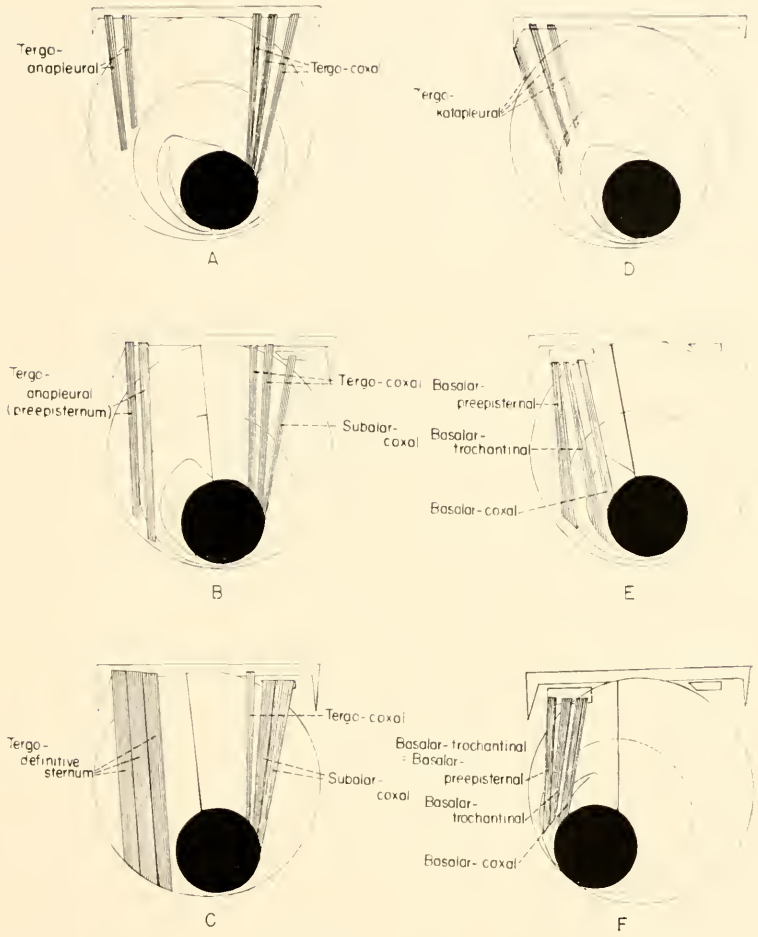

FIG. 5.—Evolution of some flight muscles. A. Posterior tergo-coxal and tergo-anapleural muscles in *Lepisma saccharina*. B. Posterior tergo-coxal, subalar-coxal (meral) and tergo-anapleural muscles in a primitive pterygote insect. Note that one of tergo-coxal muscles became a subalar-coxal (meral) muscle, and that the tergo-anapleural muscles stretched ventrad and function as indirect flight muscles. C. Posterior tergocoxal, subalar-meral and tergo-anapleural muscles in a specialized pterygote. Note that the tergo-coxal muscle reduced the number to one, that the subalar-meral and tergo-anapleural muscles have proliferated in size and become secondarily split. D. Tergo-katapleural muscles in *Lepisma saccharina*. E. Tergo-katapleural muscles in *Lepisma saccharina* have become basalar-coxal, -trochantinal and -preepisternal muscles in a primitive pterygote insect. F. The same muscles as those in fig. 5 in a cockroach. The basalar-preepisternal muscle has shifted its ventral point of attachment to the well-developed trochantin, accompanied by the reduction of the preepisternum.

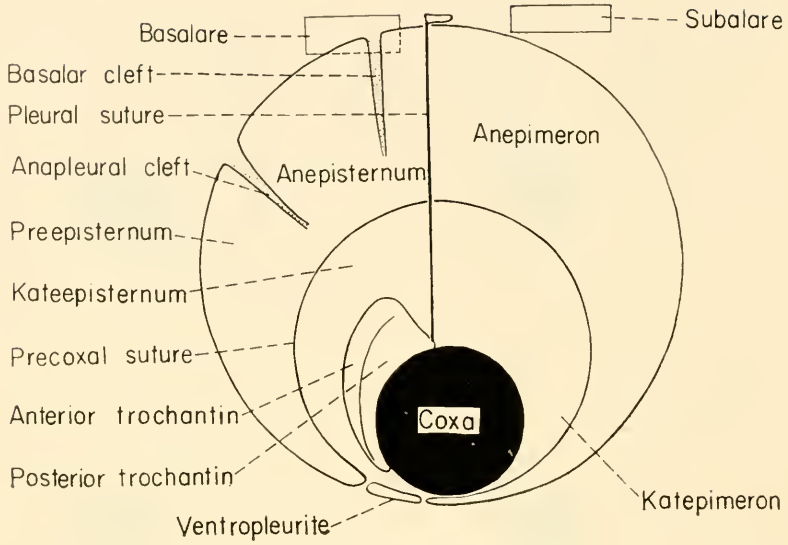

FIG. 6.—A hypothetically primitive pleural wall of the pterothorax (slightly modified from Matsuda 1960.)

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Gross Morphological Studies of the Reproductive System in Representative North American Crane Flies (Diptera: Tipulidae) [1]

BY

SAUL I. FROMMER

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1. Contribution No. 1156 from the Department of Entomology, The University of Kansas, Lawrence, Kansas; a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts.

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INTRODUCTION

The purpose of this study was to investigate the gross anatomical features, both internal and external, of the terminal abdominal segments in a representative sample of the North American tipuline fauna.

A search of the literature concerning the anatomy of the reproductive system in the dipterous family Tipulidae has shown that aside from the recent work of Byers (1961) on the genus *Dolichopeza, Tipula oleracea* is the only member of the Tipulinae in which the entire male and female reproductive system had been treated. In 1924 Bodenheimer summarized existing knowledge of the anatomy of *Tipula oleracea.*

ACKNOWLEDGEMENTS

I wish to thank Dr. George W. Byers of the University of Kansas who has guided and encouraged me through the period of this study and who has made available the facilities of the Snow Entomological Museum.

Many people have also given me assistance. I wish to thank Dr. Robert E. Snodgrass (U. S. National Museum) for his valuable communications and Dr. Ryuichi Matsuda (University of Kansas) for many stimulating conversations. To Dr. Charles P. Alexander (Amherst, Massachusetts), who assisted me in the identification of western crane flies and who has given me much useful information, I am deeply grateful. Dr. Joseph H. Camin (University of Kansas) has given me advice concerning the illustrations used in this paper.

I am grateful to Mr. and Mrs. Marvin Karp of New York, who during the summer of 1959 collected and preserved for my use many western crane flies.

Dr. Karl Stockhammer, Mr. Daniel Maiello, Mr. Alfred Dietz (all of the University of Kansas) and Mr. Cristopher Zimmerli (Basel, Switzerland) have assisted by translating certain foreign literature.

MATERIALS AND METHODS

Table I gives the names of the species of Tipulinae used in this study. Where only dried specimens were available, they were cleared in dilute (10%) potassium hydroxide, then dissected and observed in glycerine with a compound binocular microscope; specimens preserved in alcohol or Kahle's solution were not treated with potassium hydroxide. The flies were usually studied using a magnification of 100 diameters. In a few instances a phase contrast microscope giving magnifications up to 1164 × was used.

Live specimens were preserved either in 80% to 95% ethyl alcohol or in Kahle's solution; however, no final decision as to the greater worth of either as a preservative for gross morphological studies can be made at present. Specimens dissected alive in water and then transferred to alcohol (80-95%) after being opened were by far the best for gross observations. A technique which facilitates to some degree dissection of the semen pump was developed. The semen pump and its immovable apodemes and the intromittent organ were dissected out and transferred to a weak solution of chloral hydrate (one or two drops of chloral hydrate to approximately twice as much water) for one or two minutes and then removed. This procedure softens the sclerotized sheath surrounding the semen pump, from which the immovable apodemes develop, so that they can more easily be removed. In addition the sclerotized wall of the pump itself becomes less brittle and more easily handled for dissection, which proves in any case a very difficult task. Caution in timing must be observed, for too much time in chloral hydrate makes the sclerotized pump pulpy and virtually impossible to dissect.

Drawings were prepared in three ways: 1) squared grid paper 2) camera lucida and 3) microprojector. The squared grid paper method proved best for the external anatomy, while the microprojector was best for internal anatomy.

All the included figures are at least somewhat schematic, and some, as noted in the captions, are entirely so. In all the figures the letters T and S are used as abbreviations for tergum and sternum respectively. It was found important to record the type of preservation or condition of specimens from which drawings were made, for a fly that has dried frequently becomes distorted. An attempt to see all the features available in such a specimen without first relaxing it in some way and perhaps without dissection

fails more often than it succeeds. Taxonomists have often been loathe to dissect specimens, yet as Snodgrass (1904) pointed out very appropriately, "If drawings and descriptions are made of the removed parts, then the mutilated specimen has certainly done more for science than the perfect one can ever do."

TABLE I

Species studied:

An asterisk after the sex indicates the use of material preserved in liquid.

Dolichopeza (oropeza) carolus Alexander, male *, female *
Dolichopeza (oropeza) tridenticulata (Alexander), male *, female *
Brachypremna dispelleus (Walker), male, female
Megistocera longipennis (Macquart), male
Ctenophora apicata (Osten Sacken), male
Ctenophora vittata Meigen (= *angustipennis* Loew), male
Tanyptera topazina (Osten Sacken), male, female

NOTE: The specimen studied was identified as *topazina*. There is need for a reworking of the three species in the genus *Tanyptera* which occur in the United States. All may be synonymous, and if this is the case, *fumipennis* (Osten Sacken) is the valid name.

Prionocera oregonica Alexander, male *, female *
Longurio (Longurio) testaceus Loew, male
Holorusia (Holorusia) grandis Bergroth, male *, female *
Nephrotoma altissima erythrophrys (Williston), male
Nephrotoma breviorcornis (Doane), male
Nephrotoma euceroides Alexander, male *, female *
Nephrotoma ferruginea (Fabricius), male *, female *
Nephrotoma lugens (Loew), male
Nephrotoma macrocera (Say), male, female *
Nephrotoma polymera (Loew), male
Nephrotoma punctum (Loew), male
Nephrotoma xanthostigma (Loew), male
Tipula (Trichotipula) oropezoides Johnson, male *
Tipula (Trichotipula) macrophallus (Dietz), male, female
Tipula (Nobilotipula) nobilis Loew, male, female
Tipula (Nippotipula) abdominalis (Say), male, female
Tipula (Vestiplex) fultonensis Alexander, male *, female
Tipula (Arctotipula) dickinsoni Alexander, male
Tipula (Arctotipula) plutonis absaroka Alexander, male
Tipula (Yamatotipula) albocaudata Doane, male *, female *
Tipula (Yamatotipula) caloptera Loew, male, female
Tipula (Yamatotipula) concava Alexander, male
Tipula (Yamatotipula) dejecta Walker, male, female
Tipula (Yamatotipula) furca Walker, male *, female *
Tipula (Yamatotipula) jacobus Alexander, male, female
Tipula (Yamatotipula) ludoviciana Alexander, male
Tipula (Yamatotipula) sayi Alexander, male, female
Tipula (Yamatotipula) spernax Osten Sacken, male, female
Tipula (Yamatotipula) subcluta Johnson, male

Table 1—*Concluded*

Tipula (Yamatotipula) sulphurea Doane, male, female
Tipula (Yamatotipula) tephrocephala Loew, male, female
Tipula (Yamatotipula) tricolor Fabricius, male, female
Tipula (Tipula) cunctans Say, male
Tipula (Tipula) spenceriana Alexander, male
Tipula (Tipula) pendulifera Alexander, male
Tipula (Schummelia) hermannia Alexander, male, female
Tipula (Oreomyza) alia Doane, male
Tipula (Oreomyza) angulata Loew, male
Tipula (Oreomyza) appendiculata Loew, male
Tipula (Oreomyza) borealis Walker, male
Tipula (Oreomyza) doanei Dietz, male
Tipula (Oreomyza) coloradensis Doane, male
Tipula (Oreomyza) fallax Loew, male
Tipula (Oreomyza) inyoensis Alexander, male
Tipula (Oreomyza) latipennis Loew, male *, female *
Tipula (Oreomyza) pseudotruncorum Alexander, male
Tipula (Oreomyza) shoshone Alexander, male
Tipula (Oreomyza) trivittata Say, male, female
Tipula (Hesperotipula) trypetophora Dietz, male *, female *
Tipula (Eumicrotipula) chiricahuensis Alexander, male
Tipula (Lunatipula) albofascia Doane, male
Tipula (Lunatipula) armata Doane, male
Tipula (Lunatipula) australis Doane, male, female
Tipula (Lunatipula) barbata Doane, male
Tipula (Lunatipula) bicornis Forbes, male *, female *
Tipula (Lunatipula) dietziana Alexander, male
Tipula (Lunatipula) disjuncta Walker, male
Tipula (Lunatipula) dorsimacula Walker, male
Tipula (Lunatipula) duplex Walker, male
Tipula (Lunatipula) flavibasis Alexander, male
Tipula (Lunatipula) fuliginosa (Say), male
Tipula (Lunatipula) incisa Doane, male
Tipula (Lunatipula) macrolabis Loew, male
Tipula (Lunatipula) mohavensis Alexander, male
Tipula (Lunatipula) morrisoni Alexander, male
Tipula (Lunatipula) pleuracicula Alexander, male
Tipula (Lunatipula) rabiosa Alexander, male
Tipula (Lunatipula) rangiferina Alexander, male
Tipula (Lunatipula) triplex Walker, male *, female *
Tipula (Lunatipula) unicincta Doane, male, female *

TERMINOLOGY

Published observations concerning the reproductive system of crane flies date back to the works of Reaumur (1740), Dufour (1851) and Westhoff (1882). While the bibliography does not claim to be exhaustive, it contains references to the major works concerning this topic. Since the various authors have often acted

independently in their use of terms for the genitalic parts, much terminological confusion exists. Tables II and III explain the equivalents in usages of authors. These tables include terms for those parts of the reproductive apparatus that are visible without dissection or treatment with a clearing solution; three exceptions are the semen pump, its associated apodemes and portions of the vaginal apodeme. The reader should note that while the descriptions of such workers as Alexander and Byers are sound from the descriptive standpoint, the terminology used by these workers is basically taxonomic and does not pretend to be that of the morphologist.

TABLE II.—Terminological Equivalents for Male Abdominal Structures

(For notes see end of table.)

Frommer	Westhoff (1882)[1]	Snodgrass (1904)	Wesche (1906)[3]	Berlese (1909)	Bodenheimer (1924)	Sellke (1936)
1) 1st abdominal segment	1st abdominal segment	1st abdominal segment	Had the segments in Wesche's figures been labeled, his terminology would probably be comparable to mine.	2nd abdominal segment (1st lost)	2nd abdominal segment (1st lost according to Berlese)	2nd abdominal segment (1st lost according to Berlese)
2) 8th tergum	Lamella basalis supera	8th tergum		9th tergum	9th tergum	9th tergum
3) 8th sternum	Lamella basalis infera	8th sternum		9th sternum	9th sternum	9th sternum
4) 9th tergum	Lamella terminalis supera	9th tergum		10th tergum	10th tergum (not labelled in his figure)	10th tergum
Tip of 9th tergum which may take on various shapes	Processus der lamella terminalis supera			Cerci	Dreieckige Platten	Lamella terminalis supera
5) 9th sternum	Lamella terminalis infera	9th sternum		10th sternum (= periandrio; labelled p, should have been pr)	10th sternum	10th sternum
Fragmenta (= discrete sclerotized areas of the 9th sternum)						
6) Anal tubercle (= ? 10th and 11th segments)		Anal tube, but restricted to segment 10	Anal tube, but restricted to segment 10	11th segment	Analkegel (Since Bodenheimer follows Berlese's interpretation he may have thought the Analkegel represented the 11th segment)	
Dorsal or dorsolateral plates of the anal tubercle				11th tergum		
7) Sclerotizations in the walls of the genital sac, such as the "epimere" (Rees & Ferris, 1939)	Adminiculum und vesicula verbindener Bugel	V-shaped bar in roof of genital chamber lying between posterior arms (labelled a) of central vesicle		11th sternum (= epimere Rees & Ferris, 1939)	Recognizes structure but does not agree with Berlese's interpretation	

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*

(For notes see end of table.)

Frommer	Westhoff (1882)[1]	Snodgrass (1904)	Wesche (1906)[3]	Berlese (1909)	Bodenheimer (1924)	Selike (1936)
8) Basimere(s)	Appendices superae	"Pleura" [2]				
9) Telomere(s)	NOTE: Westhoff did not use a single term to embrace the appendices intermediae and the pars.	Apical appendages NOTE: Three divisions of the inner apical (inner telomere) appendage were recognized.	Forceps	Appendici	Forceps superiores	Appendix supera
Outer telomere	Appendices intermediae		Forceps superior	Appendici 1 (labelled a)	Forceps inferiores	Appendix intermedia (= Begattungsklammer): composed of pars prima, secunda, tertia and quarta
Inner telomere	Pars (1, 2, 3, and 4 = division of inner telomere)		Forceps inferior	Recognized divisions called appendici (labelled a2-a4)		
10) Adminiculum	Adminiculum	Guard of the penis (= penis sheath = 1st gonapophyses, includes lateral arms)	Penis sheath	Appendici 5 (labelled a5)	Penisscheide (adminiculum, theca)	Adminiculum
Lateral arms of adminiculum	Arme des Adminiculums					Arm (= Chitinplatte)
11) Anterior continuations of the lateral adminicular arms		2nd gonapophyses	Double apodemes			
12) Semen pump (vesica)	Vesicula centralis	Central vesicle	Sacculus ejaculatorius	Perifallo (figured this upside down)	Sacculus ejaculatorius	
Compressor apodeme	Spatha	Apodeme	Ejaculatory apodeme	Part of perifallo	Spatha, ejaculatory apodeme	
13) Aedeagus	Ruthenscheide (= integumentum, vagina)	Penis	Penis (= flagellum)	Verga flagelliforme	Penis	Penis

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*

(For notes see end of table.)

Frommer	Westhoff (1882)[1]	Snodgrass (1904)	Wesche (1906)[3]	Berlese (1909)	Bodenheimer (1924)	Sellke (1936)
14) Extended endophallus	Glans (= austulpbaren Eichel)					
15) Immovable apodemes	Aurieulae vesiculae centralis	Arms (labelled a)	Processes fused to sacculus ejaculatorius	Part of perifallo NOTE: Berlese's figure shows no separation of apodemes and semen pump	Auriculae vesiculae centralis	
Anterior apodemes					Styli	
Posterior apodemes	Styli	Arms (labelled b)				
16) Genital sac (= walls of genital chamber)	Membrana hyalina	Genital chamber			Membrane hyalina	Opening of genital sac (= Genitalhohle)

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Continued*

(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	(Snodgrass (1957)	Byers (1961)[6]
1) 1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment	1st abdominal segment
2) 8th tergum	8th tergum	8th tergum	8th tergum	8th tergum	8th tergum
3) 8th sternum	8th sternum	8th sternum	8th sternum	8th sternum	8th sternum
4) 9th tergum	9th tergum	9th tergum	9th tergum	9th tergum	9th tergum
Tip of 9th tergum which may take on various shapes	Median lobes of 9th tergum		Process		
5) 9th sternum	9th sternum	9th sternum	9th sternum	9th sternum	9th sternum
Fragmenta (= discrete sclerotized areas of the 9th sternum)	Fragmenta				
6) Anal tubercle (= ? 10th and 11th segments)	Proctiger (= 10th and 11th segments)	Proctiger or "anal segment" (= united 10th segment with cereus-bearing 11th segment)	Anal tube	Snodgrass (1935) 10th segment alone	Anal segment, 10th segment. NOTE: Evidence for an eleventh tergum is mentioned.
Dorsal or dorsolateral plates of the anal tubercle	10th tergum				
7) Sclerotizations in the walls of the genital sac, such as the "epimere" (Rees & Ferris, 1939)	Epimere				Not found in *Dolichopeza* as it is in *Tipula triplex* but may be of the same origin as the adminicular rods

Table II.—Terminological Equivalents for Male Abdominal Structures—*Continued*

(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	(Snodgrass (1957)	Byers (1961)[6]
8) Basimere(s)	Coxopodite	Basimere	Basistyle [5]	Basimere (phallic lobe origin, from parameres)	Basistyle
9) Telomere(s)	Style	Distimeres or dististyles	Dististyle	Telomere (phallic lobe origin, from parameres)	Outer dististyle
Outer telomere		Outer distimere	Outer dististyle	Outer telomere	
Inner telomere		Inner distimere	Inner dististyle	Inner telomere	
10) Adminiculum	Hypomere	See note 4	Sometimes referred to as aedeagus; when highly developed and incorporated with the gonapophyses = phallosome	Adminiculum	Adminiculum
Lateral arms of adminiculum	Included in hypomere				
11) Anterior continuations of the lateral adminicular arms					Adminicular rods
12) Semen pump (vesica)	Basal bulb of penis				Vesica
Compressor apodeme					Compressor apodeme
13) Aedeagus	Penis	Aedeagus: formed by the union of paired penis or aedeagal valves (= mesomeres)	Aedeagus	Aedeagus (phallic lobe origin, from fused mesomeres)	Penis

TABLE II.—Terminological Equivalents for Male Abdominal Structures—*Concluded*

(For notes see end of table.)

Frommer	Rees & Ferris (1939)	Crampton (1942)	Alexander (1942)	Snodgrass (1957)	Byers (1961)[6]
14) Extended endophallus					
15) Immovable apodemes	Figured but not given specific names				Anterior apodemes
Anterior apodemes					Posterior apodemes
Posterior apodemes					
16) Genital sac (= walls of genital chamber)	Genital sac				Genital sac, membranous sac

1. Westhoff (1882) used the term hypopygium for segments eight and nine and overlooked the basimeres. He named intersegmental appendages between the eighth and ninth sterna according to whether they are simple or divided as appendix basalis simplex or appendix basalis duplex. The term indusium probably refers to membrane-like evaginations at the base of the adminiculum.

2. Snodgrass (1904) used the term pleura with caution and made it clear that the term was chosen only because of the location of the structures.

3. Wesche's (1906) figure of *Tipula oleracea* is upside down.

4. Crampton (1942) discussed the term adminiculum as used by Westhoff (1882). As he interpreted Westhoff, the term adminiculum was applied to what is here called aedeagus. I do not believe that his interpretation of Westhoff was correct, since the term adminiculum was used for the supportive guide of the intromittent organ and not for a part of the organ itself.

5. Alexander (1942) cites other terms used for the basistyle; they are paramere, coxite, pleurite, gonostipes and side piece.

6. The term gonapophysis is used by Byers (1961) for a process which in this paper is designated as an outpocketing of the ninth sternum located at the base of the adminiculum. Such structures are comparable to the genital palpi or parameres as recognized by Wesche (1906).

TABLE III.—Terminological Equivalents for Female Abdominal Structures.

(For notes, see end of table.)

Frommer	(Snodgrass (1903)[3]	Wesche (1906)	Berlese (1909)	Bodenheimer (1924)
1) 1st segment	1st segment	1st segment	2nd segment	2nd segment
2) 8th tergum	8th tergum		9th tergum	9th tergum
3) 8th sternum	8th sternum	8th sternum	9th sternum	9th sternum
4) Extensions of 8th sternum (= hypovalvae)	Appendages of 8th sternum	Valvula inferior, or ventral egg guide		Extensions of 9th sternum forming the "Legerohre"
5) 9th tergum	9th tergum		10th tergum	10th tergum
6) Fragment of 9th tergum?				
7) 9th sternum	9th sternum and rudimentary 2nd gonapophyses [4] when they occur	Lamella anterior	10th sternum and mesostyli	10th sternum
8) Vaginal apodeme, furca (Byers, 1961)	1st gonapophyses			
9) 10th tergum	10th tergum and suranal plate [5]			11th tergum
10) 10th sternum? [1]				
11) 11th tergum [2]	suranal plate			
12) Infra-anal plate = 11th sternum?	Podical plates [6]		11th sternum	11th sternum
13) Cerci	Cerci	Valvula superior or dorsal egg guide	Cerei	Cerci

TABLE III.—Terminological Equivalents for Female Abdominal Structures.—*Concluded*

(For notes, see end of table.)

Frommer	Sellke (1936)	Rees & Ferris (1939)	Crampton (1942)
1) 1st segment	2nd segment	1st segment	1st segment
2) 8th tergum	10th tergum [7]	8th tergum	8th tergum or epigynium
3) 8th sternum	10th sternum	8th sternum and coxopodite	8th sternum or hypogynium
4) Extensions of 8th sternum (= hypovalvae)	Ventralen Lamellen	Gonapophysis of 8th segment	Hypovalvae or hypogynal valves [11]
5) 9th tergum	10th tergum, but not so labelled	9th tergum	
6) Fragment of 9th tergum?			
7) 9th sternum	11th sternum (Sellke misinterpreted Berlese)	See footnote [8]	9th sternum processes of 9th sternum [12]
8) Vaginal apodeme, furca (Byers, 1961)		Apodeme [below the 9th sternum and extending into the body]	See footnote [13]
9) 10th tergum	11th tergum	10th tergum	10th tergum
10) 10th sternum? [1]		See footnote [9]	
11) 11th tergum [2]		11th tergum [10]	11th tergum [14]
12) Infra-anal plate = 11th sternum?		11th sternum	Bipartite plate below the anal opening [6]
13) Cerci	Cerci	Cerci	Cerci

1. If we recognize the infra-anal plate as the true eleventh sternum then the tenth sternum is represented by a membranous area between sternum nine and eleven.

2. No evidence of an eleventh tergum was found. See discussion in text.

3. This earlier interpretation for those parts called gonapophyses is no longer maintained. Snodgrass (personal communication) now believes in a sternal rather than an appendicular origin for these parts.

4. The rudimentary second gonapophyses (Snodgrass, 1903) are two chitinous rods that arise close to the lower ends of the ninth tergum and converge posteriorly where they unite in a continuous plate. This plate is equal to sternum nine.

5. The suranal plate (Snodgrass, 1903) is equal to a distalmost, triangular tip of the tenth tergum. Crampton apparently considered it the eleventh tergum and used the term suranal, supra-anal plate or epiproct for dorsal-plates found in those instances where the tenth and eleventh segments become indistinguishably fused. The term subanal plate or hypoproct was used by Crampton for comparable ventral plates.

6. Snodgrass (1903) called the plate found below the anal opening the podical plate. Crampton (1942) believed that this plate might bear some relation to paraprocts.

7. It is clear from Sellke's words that he meant to follow Berlese's terminology; however, he misinterpreted Berlese.

8. A sclerotized portion of sternum nine is labelled gonapophysis of segment nine figured for *Limonia sciophila* (Osten Sacken) but not for *Tipula (Lunatipula) reesi* Alexander. This apparently is supposed to represent two lateral plates which are fused to each other and to the ventral surface of the ninth sternum.

9. The text states that the tenth sternum is absent in crane flies, but figure 86 (Rees and Ferris, 1939) is labelled tenth sternum. Figure 89 is labelled according to the text.

10. In *Limonia sciophila* (Osten Sacken) a fragmentum which may represent a part of the tenth tergum is labelled eleventh tergum; such a sclerite is not found in *Tipula (Lunatipula) reesi* Alexander.

11. Crampton (1942) suggested the possibility that the hypovalvae may represent the ventral valves of a true ovipositor. Since the egg-laying apparatus in Tipulidae derives from the dorsal cerci and ventral hypovalvae he felt that the term ovipositor should not be used for it. He proposed the term oviscapt or ovicauda, because he felt that the two structures, although having analogous functions, were not homologous, that is, not homologous to a supposedly appendicular, orthopteroid ovipositor. Since the ovipositor of orthopteroids may still be shown, as Matsuda (1957) believes, to be sternal in origin and although this structure is of dual origin in crane flies, I prefer to follow Byers (1961) in retaining the present terminology to avoid possible additional confusion.

12. Crampton (1942) states that in some tipulids processes of the ninth sternite, which I am interpreting as sclerotized portions of the ninth sternum may represent the dorsal valves of a true ovipositor.

13. Crampton believed that the vaginal apodeme might represent fused first gonapophyses (appendicular origin of the female ovipositor).

14. Crampton (1942) figured the terminal abdominal segments of a female tipulid *Clytocosmus* in which "the cercus-bearing eleventh segment (with which the anus-bearing telson has united) is apparently represented largely by the distinct, though small sclerites at the bases of the cerci, ce." The tergal portion of the eleventh segment was further identified by an area posterior to a dotted line separating the distalmost part of a plate continuous with the tenth tergum. Rees and Ferris (1939) found a similar situation in *Limonia sciophila* (Osten Sacken) and interpreted these parts in the same way.

THE MALE

The parts of the male which are associated with the reproductive apparatus and which are for the most part heavily sclerotized are 1) the eighth sternum and its appendages when present, 2) the ninth segment (hypopygium, of authors), 3) the parameres, comprising the single basimere and two telomeres on each side, 4) the aedeagus, 5) the adminiculum, 6) the genital chamber, including the so-called genital sac, 7) the semen pump (the modified endophallus), 8) the compressor apodeme of the semen pump, 9) the immovable apodemes (two anterior and two posterior) of the semen pump, 10) the semen pump brace and its extension, when present, the brace of the ejaculatory duct. By reference to the figures, the parts listed can be identified.

PARAMERES AND AEDEAGUS

The parameres in tipuline crane flies probably develop in the sternal portions of the intersegmental membrane between segments nine and ten. In the adult they are divided into two primary parts, the proximal basimere and the distal telomere. Furthermore, in crane flies the telomere is divided again into the outer and inner telomeres. The actual protrusive, or intromittent organ has been called the aedeagus by Snodgrass (1957). There is evidence that in some crane flies the sclerotized portion of the protrusive organ actually sheaths an inner flexible tube which may be endophallic in origin. According to Snodgrass (1957), the aedeagus and parameres develop from a pair of phallic lobes which divide at first into secondary lobes or phallomeres, the inner pair called mesomeres, the outer pair called parameres. The mesomeres then become hollowed on their opposed surfaces and unite with each other to form a tubular, median organ, the aedeagus. In dissecting the intromittent organ of *Dolichopeza tridenticulata* and *Dolichopeza carolus* I have noticed within this fine sclerotized outer tube still another tube. The inner tube is able to withstand the action of potassium hydroxide. At first it appeared only as a hyaline tube concealed by the more sclerotized portion of the aedeagus and visible only after its rupture; later I examined specimens in which this innermost tube projected from the tip of the aedeagus. While this inner tube may represent an aedeagus, ensheathed by a sclerotized thecal covering, it is more likely an extension of the endophallus. I have in one instance removed this inner tube and observed it with the phase contrast microscope (at 1164×), and it appeared

to be a double cylinder. Snodgrass (1935, p. 590, Fig. E) figures an intromittent organ which is in essence comparable to that of *Dolichopeza.* In other crane flies studied I have not been able to demonstrate this inner tube. It is possible that in these crane flies the inner tube has become inseparably connected to the inner wall of the sclerotized intromittent organ. It is equally possible that in these species the endophallus is not extended. The entire intromittent organ in the majority of crane flies studied, while quite strong and flexible, is of a very small bore; this may account for the difficulty in distinguishing the inner from the outer tubes.

The recent investigations of Neumann (1958) with *Tipula oleracea,* in which microtome sections were studied, do not show the development of such an inner endophallic tube.

It is impossible to overstress the need for abundant comparative material in a morphological study such as this. The inner tube found in *Dolichopeza* may be present within the aedeagus of *Tipula* (*Yamatotipula*) *jacobus.* In the European crane flies studied by Westhoff (1882) this may also be the case. The figures given by Westhoff (Figs. 50, 59, 60, 61) for *Tipula hortulana* Meigen, *Tipula sinuata* Fabricius, *Tipula winnertzi* Egger and *Tipula varipennis* Meigen show a structure at the extreme tip of the aedeagus (penis, of authors) which resembles that of *Dolichopeza* and *Tipula jacobus.* Westhoff stated that this structure, designated as an "austulpbaren Eichel" (= glans), had already been described by Dufour (1851) for *Tipula oleracea* Linnaeus. The glans as described by Westhoff may take various shapes. It may be drawn out to a fine point as in *Tipula oleracea* Linnaeus; in *Tipula sinuata* Fabricius it is less fine and less drawn out; and in *Tipula varipennis* Meigen and *Tipula hortulana* Meigen it is long and blunt. In the last two it is characterized by possessing a ring of fine grooves. These ring-like grooves may serve to secure the aedeagus within the bursa copulatrix. This information supports the contention that an inner tube exists within what has been called the penis. While the terms theca and endotheca could be used for the sclerotized parts of the intromittent organ of *Dolichopeza,* such use is arbitrary and only suggests one possible ontogenetic explanation for the final structure of the intromittent organ. It would be just as easy and perhaps preferable to visualize the theca and endotheca as comparable to the aedeagus and endophallus (Snodgrass, 1957) and the innermost tube as merely an extension of the endophallus. Text figure 1 indicates these supposed relation-

ships in diagrammatic form. Until ontogenetic studies of development of the reproductive system in crane flies are made, a final decision concerning the homologies of these parts must be deferred.

In the Tipulinae the parameres are found in one of two primary positions. In the first type the basimere is completely free from the ninth sternum as in *Brachypremna and Megistocera,* and in the second it is either partially or wholly fused with the ninth sternum as in *Tipula (Lunatipula) triplex* Walker (Figs. 6, 9, 10).

In order to give correct morphological names to the parts comprising the intromittent organ and semen pump it would be necessary to know the exact manner in which these parts have developed. Since this is not yet known for the Tipulidae a flexible terminology for the component parts is given.

Following Snodgrass (1957) we may assume that the aedeagus is formed from fused mesomeres. The two alternatives following aedeagus formation are, 1) formation of a sheath around the aedeagus and 2) enlargement of the endophallus. Figure a of text figure 1 diagrammatically portrays the intromittent organ after fusion of mesomeral lobes. At this point we find the aedeagus (Ae) and, within, the endophallus (Enph 1). Note the connection of endophallus and ejaculatory duct (ED). In Figure b the endophallus (Enph 1) has enlarged to form an extension, labelled (Enph 2), which forms a second tube within the first of figure a. The inner portion of this endophallic extension is cross-hatched in the figure. In figure c the inner layer of the endophallus is not cross-hatched, but the organ is at the same stage as in figure b. Figure d shows the specialization of endophallus to produce the bulb of the semen pump and is labelled (Enph 1). Figure e gives a schematic representation of the semen pump and intromittent organ. The cross-hatched area (X), of this figure represents the site of the compressor apodeme. Note that the aedeagus (Ae) is continuous with the membranous sac at the base of the bulb. The base of the membranous sac while not labelled is represented by the stippled ring of tissue at the base of the semen pump. Figure f is a transverse section of the semen pump and the compressor apodeme (CA).

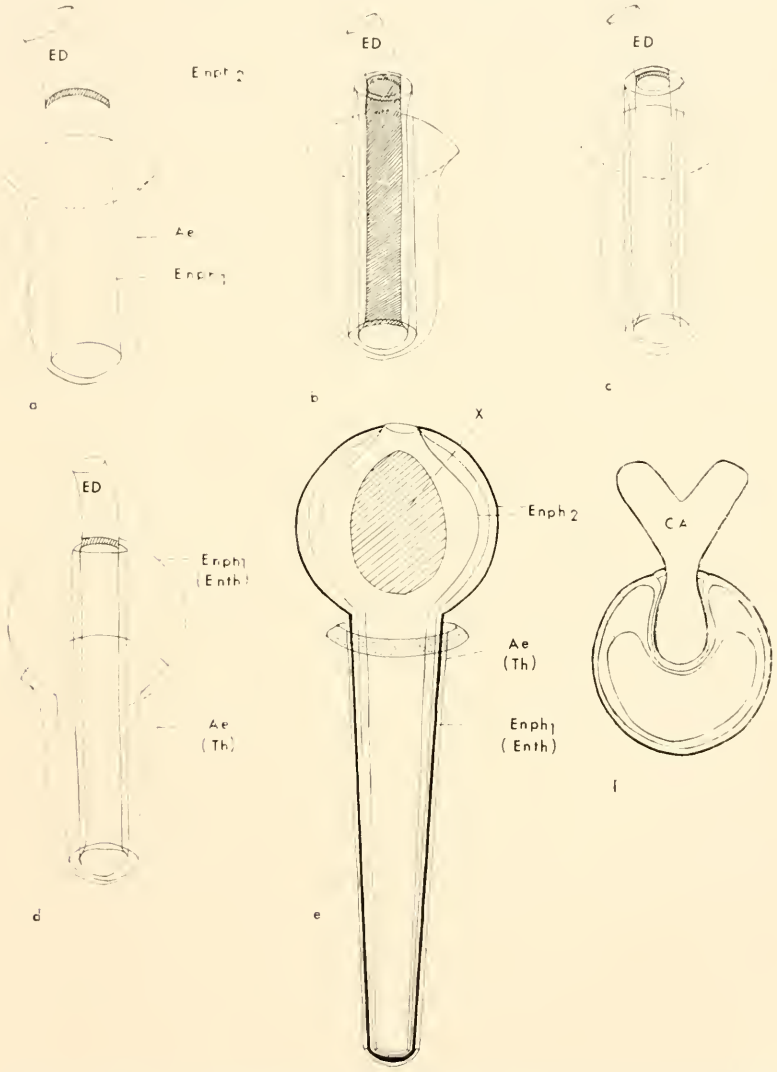
These figures as just explained give the terminology which should be used in the case where enlargement of the endophallus can be shown to have taken place. Such a situation seems to obtain in *Dolichopeza.*

If it can be demonstrated that a thecal sheath forms about an aedeagus and that endophallic enlargement does not occur, then

what was called aedeagus should be called theca (Th) and what was called endophallus should be called endotheca (Enth).

The aedeagus would then be what was called endophallus two (Enph 2) and within it an endophallus (not labelled).

The presence of an inner tube within the sclerotized intromittent organ has not been demonstrated for species other than those in



TEXT FIGURE 1.—A schematic and hypothetical representation of the development of the intromittent organ and the semen pump in the Tipulinae.

the genus *Dolichopeza*. If the reader ignores those parts of the figures showing the endophallic enlargement, no difficulty should be had in visualizing the development in all the other Tipulinae.

ADMINICULUM

Caudally, in the median line, there is a strengthened portion of the intersegmental membrane between segments eight and nine, the adminiculum (Figs. 10, 11, 12). This structure serves as a support and guide for the intromittent organ. It is continuous with the ventral wall of the genital chamber and is equipped with muscles extending anteriorly to the antecosta of the ninth sternum. By contraction of these muscles the adminiculum is drawn toward the ninth tergum.

The adminiculum is usually most conspicuously developed in its median portion, although it may have on either side various prongs or arms; these arms may be free or may lie in the walls of the genital chamber. The lateral arms and the median body do not represent gonapophyses (Snodgrass, 1904) but are merely sclerotized portions of the intersegmental membrane. The thickenings of the genital chamber extending anteriorly from the adminiculum have been called adminicular rods (Byers, 1961). Such thickenings may be seen in the genus *Dolichopeza* and in *Tipula (Nobilotipula) nobilis*. Adminicular rods seem to support the walls of the genital sac and, in the case of *Dolichopeza* and *Tipula (Nobilotipula) nobilis* where they extend to the semen pump, serve as a fulcrum upon which the semen pump rotates (Fig. 41). The adminiculum can be observed to assume many shapes providing excellent characters for the systematist (Byers, 1961).

Loew (1873) believed the adminiculum was the actual intromittent organ and applied to it the term "Copulationsglied."

GENITAL CHAMBER AND GENITAL SAC

The genital chamber is formed by an invagination of the intersegmental membrane between the ninth and tenth segments. The thin walls of this chamber are concealed within the abdominal segments, and it is usually found as in *Tipula (Lunatipula) triplex* within the ninth segment; however, when the intromittent organ becomes greatly lengthened as in *Tipula (Trichotipula) macrophallus*, a slender portion of the genital chamber may extend forward well into the thorax. The term genital sac has been used for the walls of this chamber. The intromittent organ is found within the chamber and when it is withdrawn becomes bowed, its elasticity

causing the walls of the chamber to become taut (Text Fig. 2). The aedeagus and the wall of the genital chamber are contiguous at the base of the aedeagus (Text Figs. 3a, b). The dorsal wall of the genital chamber may also be sclerotized to a greater or lesser extent, and it is to such a sclerotization that Rees and Ferris (1939) gave the name epimere. This sclerotization takes various forms, for example a transverse bar in *Tipula (Vestiplex) fultonensis,* and a broad Y-shaped sclerotization (epimere) in *Tipula (Lunatipula) triplex;* alternatively the sclerotization may be absent, as in the genus *Dolichopeza.*

Dufour misinterpreted the true nature of the genital sac, as he thought it was fused to the intromittent organ. It is clear, however, that the intromittent organ is so fused only at its base where the semen pump develops.

Semen Pump and Compressor Apodeme

The semen pump (Text Figs. 1, 3) is derived from a specialized portion of the endophallus which is bulblike. Its wall is invaginated at one point, and in this invagination is found a movable apodeme, the compressor apodeme, so called by virtue of its function. This apodeme has been called the piston adopeme by Abul-Nasr (1950) and the ejaculatory apodeme by Wesche (1906). Keuchenius (1913) was unable to interpret the finer detail of this structure. I have been able to dissect it under the binocular microscope and observe it at 100× magnification. Within the bulb are found a number of membranes. At the position where it is invaginated, the hardened wall of the pump gives way to a flexible membrane which allows the compressor apodeme to make its movements. The outer wall of the endophallic enlargement arises from a point caudal (morphologically anterior) to the compressor apodeme at the connection of the ejaculatory duct and runs through the body of the semen pump out through the intromittent organ then invaginates and retraces its path into the pump, finally making connection with the ductus ejaculatorius. (See Text Fig. 1, where the probable derivations of the parts of the intromittent organ are indicated diagrammatically; compare the schematic drawings of the semen pump and intromittent organ in Text Figs. 1e and 3a.)

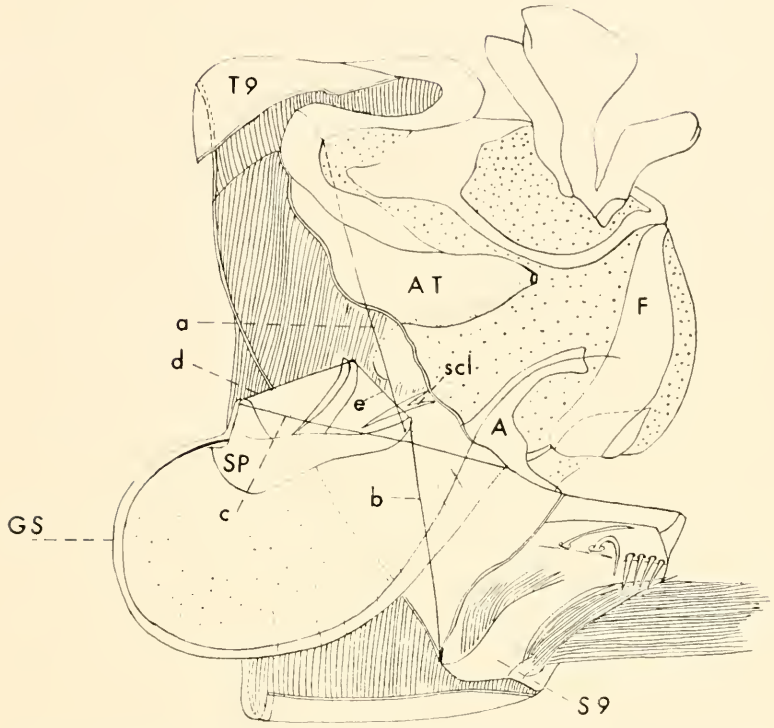
Whether the compressor apodeme is derived from the wall of the semen pump (endophallus) or from some other source, as proposed by Abul-Nasr (1950) for the anisopodid, *Anisopus fenestralis,* is a question which cannot be resolved until a study of its ontogenetic development is made.

IMMOVABLE APODEMES OF THE SEMEN PUMP

If one dissects out the semen pump of a crane fly, there can be observed in addition to the aforementioned compressor apodeme four other apodemes. These envelop the body of the pump and serve for the attachment of muscles on both sides of the compressor apodeme, enabling this apodeme to make its movements. In addition, there are three sets of muscles attached to the immovable apodemes which serve to rotate the semen pump (Text Fig. 2). From each of the arms of the anterior immovable apodemes the first set of these muscles extends to either side of the base of the adminiculum, and by their contraction the semen pump rotates in the sagittal plane, resulting in a caudal extension of the intromittent organ. From each of the arms of the immovable posterior apodemes the second and third set of muscles arise. The first set extends to the antecosta of the ninth sternum and upon contraction the semen pump rotates in the sagittal plane, withdrawing the intromittent organ into the genital chamber. The second set of muscles extends to the dorsalmost edge of the ninth sternum, where it joins the ninth tergum. Contraction of these muscles causes the semen pump to rotate in the sagittal plane resulting in a caudal extension of the intromittent organ (Text Fig. 2). The immovable apodemes are developed from a portion of the dorsal wall of the genital chamber, which envelops the body of the semen pump.

The semen pump (pompetta, Abul-Nasr, 1950), compressor apodeme (piston apodeme, Abul-Nasr, 1950), immovable apodemes and intromittent organ (penis, Abul-Nasr, 1950) of a crane fly such as *Tipula* (*Lunatipula*) *triplex* bear a striking resemblance to similar structures in the anisopodid figured by Abul-Nasr (1950). If these structures are to be thought of as homologous, as is suggested by their similarity in form, location, and probable function, then certain differences in the interpretation of the parts become evident.

Abul-Nasr (1950, p. 376) states that the penis "is composed of a filamentous cuticular tube which is devoid of cellular coat except at its most proximal part, where the penis tube is surrounded by the pompetta." He makes no mention anywhere in his paper of an inner tube, such as occurs in the genus *Dolichopeza*. The anisopodid which he studied is a very small fly, and it seems that if such an inner tube exists in this fly it could easily have been overlooked, especially when we consider the difficulty encountered in locating it in *Tipula*.



Text Figure 2.—Semidiagrammatic parasagittal view of the terminal abdominal segments of a male crane fly drawn to show muscle attachments necessary for the movements of the semen pump, compressor apodeme, and intromittent organ. Muscles (d) and (e) move the compressor apodeme: contraction of muscle (d) compresses the lumen of the semen pump expelling semen while at the same time the "heel" of the compressor apodeme within the pump closes the opening into it from the ejaculatory duct; contraction of muscle (e) reopens the entrance into the semen pump and causes a partial vacuum which can draw additional semen into the bulb of the pump. Muscles (a), (b), and (c) are concerned with rotation of the semen pump resulting in movements of the intromittent organ: contraction of (a) and (c) results in a counter-clockwise movement of the semen pump and eversion of the intromittent organ; contraction of (b) results in a clockwise rotation of the semen pump and retraction of the intromittent organ. d = muscles from compressor apodeme to anterior immovable apodeme; e = muscles from compressor apodeme to posterior immovable apodeme; a = muscle from posterior immovable apodeme to the dorsalmost part of sternum nine where it meets the ninth tergum. b = muscle from posterior immovable apodeme to the antecosta of sternum nine. c = muscle from anterior immovable apodeme to base of adminiculum; AT = anal tubercle; A = adminiculum; F = fragmentum of sternum nine; SP = semen pump; scl = sclerite in dorsal wall of genital chamber (epimere, Rees and Ferris, 1939); GS = genital sac. (Redrawn and modified from Rees and Ferris, 1939.)

Then again, the semen pump and associated structures may not develop in the same way in tipulines and anisopodids. Aside from the invaginated portion of the semen pump (thin elastic tissue, Abul-Nasr, 1950) which enables the movement of the compressor apodeme, Abul-Nasr makes no mention of any other membranes within the body of the pump itself, although his figure (p. 370) suggests some others. He states that the piston apodeme "springs from a large cuticular structure in the shape of a bird's sternum without a keel." He goes on to say that this structure "serves as a hood over the pompetta and provides a suitable surface for the attachment of muscles responsible for the movements of the piston." Unfortunately I have not been able to understand fully his explanation of the derivation of the pompetta and the piston apodeme. His figures leave something to be desired. Nevertheless, no such hood occurs in the Tipulinae, and the muscles which work the compressor apodeme extend to the immovable apodemes. Further, Abul-Nasr describes the semen pump as a "small cuticular box with two lateral alate apodemes." He does not make it clear whether these apodemes arise as outgrowths of the pompetta itself or are, as I believe occurs in the Tipulinae, developed from cuticular thickenings of the dorsal wall of the genital chamber.

In the work of Wesche (1906) we find a discussion concerning movements of the semen pump and the intromittent organ. Wesche's figure (Plate 24, Figure 24) is reproduced upside down, and in addition his Figure 26 is both crudely and improperly drawn, failing to show the anterior immovable apodemes and showing the compressor apodeme at a right angle to its normal position at rest. Muscles are figured attached to this apodeme; however, their origins are not diagrammed. The median portion of the adminiculum is termed "theca" while portions of the lateral arms of this body are called the "apodemes of the penis, the double apodeme, the great apodeme, and the forcipes interiores."

A consideration of Wesche's paper convinces me that he only partially understood the working mechanism of the semen pump and the movements of the intromittent organ. Since he made his observations from materials placed on slides, it is easy to see how he could have drawn improper conclusions and figured the parts incorrectly.

Bodenheimer (1924) criticized Wesche's interpretation concerning the mechanics of the semen pump and offered his own observations. He pointed out that Wesche ascribed great importance to the compressor apodeme, which, as Bodenheimer interprets Wesche,

causes a rotation of the semen pump and is thereby able to open and close its opening. Bodenheimer believed that such a function (probably referring to the opening and closing of the lumen of the semen pump) is carried out by smooth or striated musculature and not by skeletal parts. Hence it can be seen that it did not occur to Bodenheimer that the compressor apodeme could actually close the opening into the semen pump. In an earlier section (p. 409) of his paper, Bodenheimer criticizes Westhoff's (1882) idea that the semen pump is a depot for the storage of sperm and states that its vesicular inflation ("blasige Auftreibung") is more likely due to the action of the numerous muscles which are attached to it. Though Bodenheimer granted that the semen pump might have a temporary storage function during copulation, he thought even this unlikely. It seems that Bodenheimer attributed a semen pumping function to this structure, but he does not state this outright. He attributes the outward protrusion of the intromittent organ to the concerted action of the so-called "Muskelpresse" of the posterior abdomen. Whether he recognized the function of the muscles of the immovable apodemes which rotate the semen pump cannot be determined.

The semen pump is given support from the rear by a small median brace (Figures 48, 53) which runs from the bulb of the semen pump at the level of the entrance of the ductus ejaculatorius to the innermost posterior margin of the sheath of the pump. This brace lies in the mid-line, between the posterior immovable apodemes. Its length varies in different species and is in some quite short. In these latter species the enveloping sheath of the pump is of necessity snugly fit around the semen pump, but in species where the brace is long one can see a distinct separation between semen pump and sheath. This seems to be a point worth stressing since when the brace is short and the sheath close-fitting, the apodemes which develop from this sheath may appear to be formed from the body of the pump. The study of many different species has, however, made this relationship clear.

At times the brace is continued up along the posterior (morphologically dorsal) surface of the ejaculatory duct at the point of its union with the semen pump. I have called this extension the brace of the ejaculatory duct (Figures 51, 52, 53); however, it does not seem to have an independent derivation.

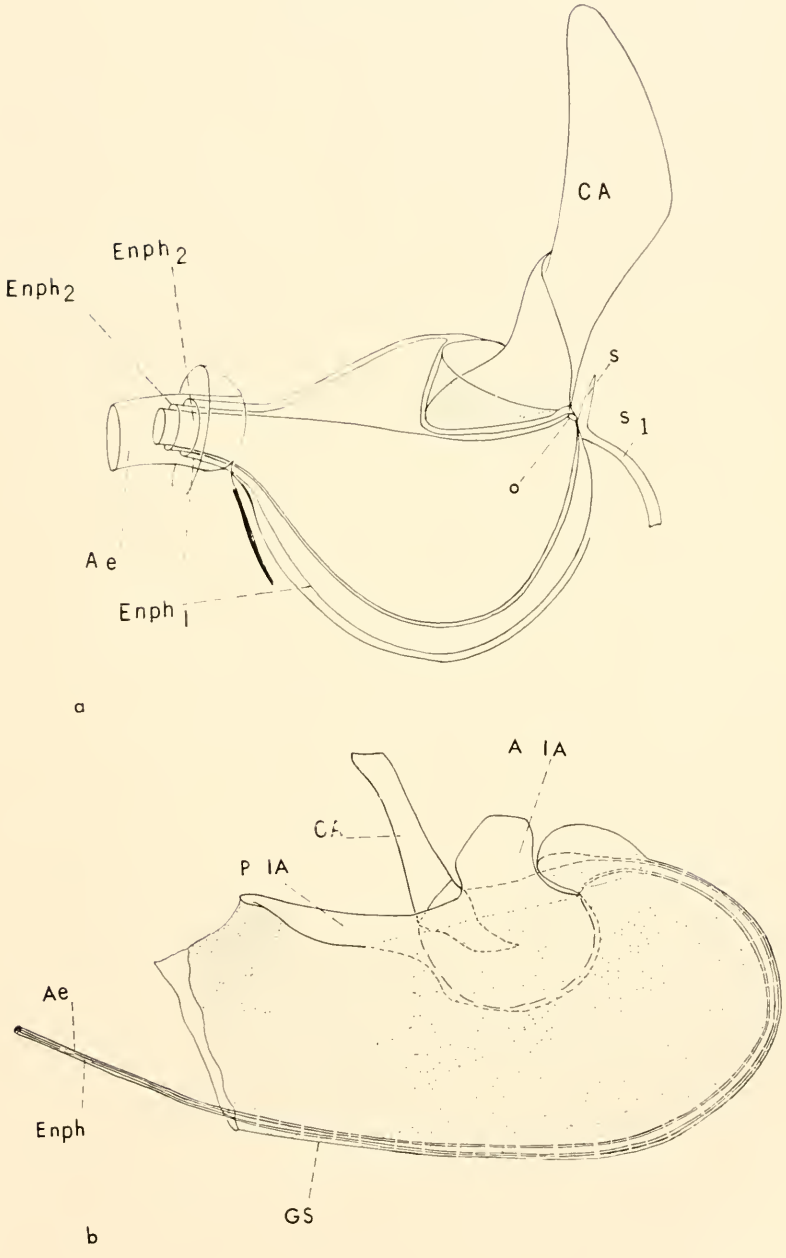
Types of Semen Pump—Intromittent Organ Complex

Three distinct types of arrangements of the semen pump and intromittent organ may be observed in the tipuline crane flies studied:

TEXT FIGURE 3

TEXT FIGURE 3.—FIG. a.—Schematic drawing of semen pump and compressor apodeme in a crane fly such as *Dolichopeza*. In species other than those of the genus *Dolichopeza* the presence of an endophallic enlargement (Enph $_2$) within the tube-like intromittent organ (Ae and Enph $_1$) could not be definitely established. Gross dissection of the body of the semen pump of species in the genus *Tipula* did suggest the development of an endophallic enlargement; however, figures (Neumann, 1958) of sagittal sections of the semen pump of *Tipula paludosa* do not show any development of the endophallus. Note the sclerotized bar (S $_1$) from the median line of the posterior apodeme (not figured) extending to the semen pump (O) where the pump joins the ejaculatory duct; and the brace of the semen pump, a sclerotized bar (S) which is a continuation of S $_1$. CA = compressor apodeme; Ae = aedeagus; Enph = endophallus; Enph $_2$ = endophallic enlargement. FIG. b.—Schematic drawing of semen pump and associated structures. *Note:* 1) the figure does not show any endophallic extension. PIA = posterior immovable apodeme; AIA = anterior immovable apodeme; GS = genital sac.

TEXT FIGURE 3



Type I—Intromittent organ arises as an unbowed extension of the semen pump. Examples of this type are *Brachypremna dispellens* (Figs. 6, 51, 52) and *Megistocera longipennis.*

Type II—Intromittent organ only slightly bowed. Anterior immovable apodemes much enlarged and united along their median basal line but slightly separated distally. A second pair of apodeme-like structures (I have only seen cleared specimens of this and am unable to say whether muscles are attached to these processes in the living fly) is found lateral to the semen pump. The basal portion of the aedeagus is specialized into an elongate and somewhat club-shaped process. This type has been found in only one fly of all those studied, *Tipula (Nippotipula) abdominalis* (Figs. 1, 7).

Type III—This form is by far the most common and was found in all other flies studied (Text Figure 3b). In this type the intromittent organ is strongly bowed, and among the species studied this condition finds its greatest expression in the genus *Nephrotoma* and in *Tipula (Trichotipula) macrophallus,* in which the intromittent organ extends anteriorly from the semen pump in the longitudinal axis of the body, makes a short arc, and then continues back towards the terminal abdominal segments.

Torsion: Temporary and Permanent

Sellke (1936) describes what might be called a temporary torsion of the male terminal segments during copulation. After copulation these segments return to their normal positions.

No good evidence of permanent torsion (rotary inversion or "transinversion" in the sense of Crampton 1942) has been seen in any of the crane flies studied except *Brachypremna dispellens* and *Megistocera longipennis.* I have been able to study only two specimens of the former and one of the latter, and in all these the ninth segment appeared to have rotated while the tergum and sternum of segment eight were only partially rotated (about 90°). Dr. C. P. Alexander (personal communication) has examined additional specimens and states that the rotation does not seem to be complete, that is, 180°. In *Brachypremna* and *Megistocera* the anal tubercle was observed to be in a ventral position and the adminiculum in a dorsal position. The internal organs of these dried specimens had already disintegrated, hence I could find no evidence of a looping up of the ejaculatory duct from left to right over the top of the hindgut. Crampton (1942: 87) refers to the work of Edwards (1924), who described a permanent torsion in the tipulid

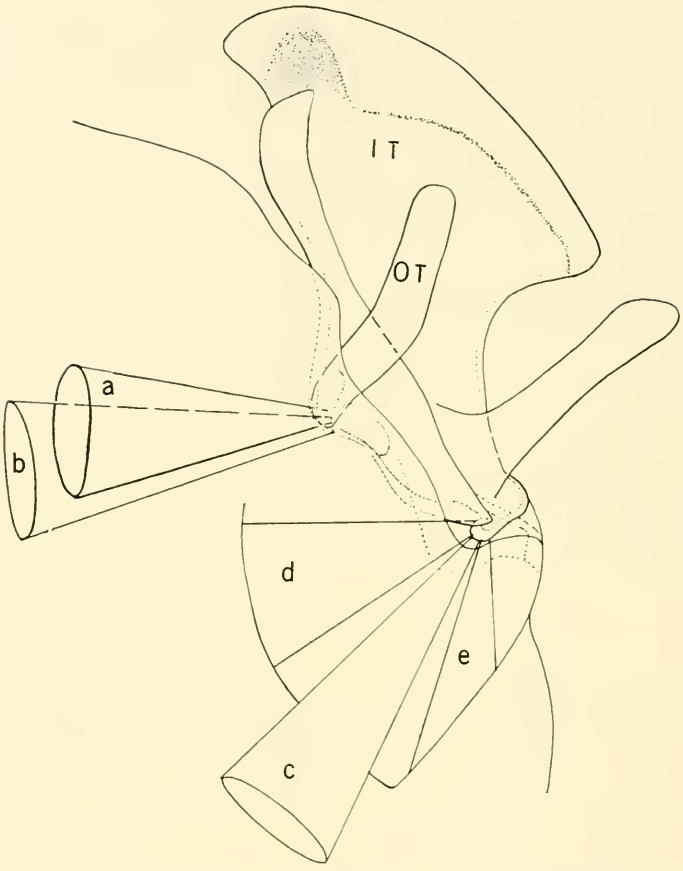
Styringomyia and knew of only two other cases of complete and permanent torsion in the Tipulidae, occurring in the genera *Molophilus* and *Amphineurus*. He mentioned in addition a case of incomplete torsion in the genus *Micromastix* (probably a synonym of *Longurio*).

Abul-Nasr (1950) discusses torsion in an anisopodid. The relative positions in the adult anisopdid, save the anal tubercle, are similar to those found in an adult crane fly such as *Tipula*, the major difference being only in the position of the anal tubercle, which in the anisopodid adult is ventral but which in the adult tipulid remains dorsal. By comparing the tipulid with the anisopodid I can see no visible evidence of any torsion in the adult crane fly other than the position of the ductus ejaculatorius relative to the compressor apodeme. One possible explanation for this phenomenon is that if the endophallus alone were to make a rotation of 180° in the development of the fly the unchanged position of the anal tubercle would be explained. Here again developmental studies may elucidate the situation.

Origin of the Telomeres

We have already considered the development of the parameres and discussed their division into two primary parts, the basimere and telomere. Workers have in the past attributed the origin of these parts to appendages of the genital segments. As a result of such thinking, names such as coxopodite and gonocoxopodite have been given to the structure here recognized as the basimere. Matsuda (1958) gives a history of the problem concerning the origin of male genitalia.

A dissection of the ninth abdominal segment reveals the origins and insertions of the various muscles which move the two telomeres. From both the basimere and the antecosta of the ninth sternum (Text Figure 4) muscles extend to the inner telomere. If the basimeres were of appendicular origin, one might expect muscles which operate the telomere to spring from the basimere alone; on the other hand if the parameres are intersegmental in origin, we might expect muscles which run to them to arise at the antecosta of the ninth sternum, and then, with the secondary divisions of the parameres, muscles might run to the basimere as well. Because other workers have indicated movement of muscle attachments, it is difficult to arrive at any final decision concerning this argument. In other words muscle attachments may not be the best criterion for settling this problem.



TEXT FIGURE 4.—Telomeres of *Tipula (L.) triplex*, male. OT = outer telomere; IT = inner telomere; (a) = muscle from outer telomere to antecosta of the ninth sternum; (b) = muscle from inner telomere to antecosta of the ninth sternum; (c) = muscle from inner telomere to antecosta of the ninth sternum; (d) and (e) muscles from the inner telomere to the rim of the basimere.

ANAL TUBERCLE OF THE MALE

In the male fly the last distinctly recognizable segment is the ninth. There is, however, a fleshy tubercle at the apex of which opens the alimentary canal. In some flies studied, this tubercle appears sclerotized both dorsally and laterally, in some only laterally. Berlese (1909) figured such plates and considered them as evidence of an eleventh tergum. This of course is due to his idea that the first abdominal segment was lost in the crane flies. It would appear as if Berlese, trying to identify the basic eleven abdominal segments, started his count from the rear. In any case no distinct separation

into tenth and eleventh segments is visible. In keeping with the line of reasoning which is proposed for these segments in the female, one might imagine a decrease in sclerotization of the tenth and eleventh segments with reduction in size. Because we can as yet come to no definite conclusion concerning the nature of these segments in males I have called this structure the anal tubercle and assigned it tentatively to segments ten and eleven. Whether the sclerotizations in the wall of the tubercle are tergal elements (of either or both segments) or merely secondary in nature cannot as yet be decided.

Gross Internal Anatomy of the Male Reproductive System

The gross internal anatomy of the remaining parts of the male reproductive system is represented in Figures 47, 50, 55-58, 91. The parts of this portion of the system are as follows: 1) a pair of testes, 2) a pair of vasa deferentia, 3) the seminal vesicle, 4) a pair of accessory glands, 5) the ejaculatory duct and a vesicular gland at the distal end of the ejaculatory duct.

Table IV shows the terminology used by various workers who have studied the tipuline reproductive system.

A comparison of my Figures 55 and 56 with those of Dufour (1851) and Keuchenius (1913) shows that the vasa deferentia may or may not be swollen at some point along their lengths. Although I have made no histological studies of these parts, the descriptions by Keuchenius (1913) and Bodenheimer (1924) seem to agree with my observations, the only departure being the possible lack of a swollen portion along the length of the vasa deferentia. Since these other workers studied but one species (*Tipula oleracea*) they could of course not see such variation. In a freshly-dissected fly, it is readily observed that the vasa deferentia come close together at some point and from there on run side by side as one, coiling in some flies. They have not been found to fuse with each other in any of the flies studied, although Byers (1961) believed this occurred in *Dolichopeza polita*. In specimens of *Dolichopeza tridenticulata* it seems to me that they are separate as in all other Tipulinae examined. Because they are very close to each other and because each is enveloped by a muscle coat which is further covered by a layer of fatty tissue (tunica adipo membranacea, Keuchenius, 1913) this separation is not readily noticed. Table V gives the results of observations of these parts. Another variation that may readily be observed is the degree of coiling of the ejaculatory duct.

TABLE IV.—Terminological Equivalents for Male.

	INTERNAL REPRODUCTIVE ORGANS			
	Frommer	Dufour (1851)	Keuchenius (1913)	Bodenheimer (1924)
1.	Testes	Testes	Testes	Testes
2.	Vas deferens	Vas efferens Vesicula seminalis Vas deferens	Vas deferens	Vas efferens Vesicula seminalis Vas deferens
3.	Seminal vesicle	Bladdery widening which forms the commencement of the ductus ejaculatorius	Bladdery widening which forms the commencement of the ductus ejaculatorius	Bladdery widening which forms the commencement of the ductus ejaculatorius
4.	Ductus ejaculatorius (seminal duct, Byers, 1961)	Ductus ejaculatorius	Ductus ejaculatorius	Ductus ejaculatorius
5.	Accessory glands	Accessory glands	Accessorial tubes	Abdominale Drüsen
6.	Vesicular gland (Byers, 1961)			

Table V.—Nature of the vas deferens and ejaculatory duct in some representative crane flies.

Species Studied	Vas deferens	Ejaculatory duct
Dolichopeza (Oropeza) tridenticulata	not swollen	loosely coiled
Dolichopeza (Oropeza) carolus	not swollen	loosely coiled
Prionocera oregonica	swollen	uncoiled
Tipula (Orcomyza) latipennis	swollen	uncoiled
Tipula (Vestiplex) fultonensis	swollen	closely coiled
Tipula (Lunatipula) triplex	not swollen	closely coiled
Tipula (Lunatipula) bicornis	not swollen	closely coiled
Tipula (Hesperotipula) trypetophora	swollen	closely coiled
Holorusia (Holorusia) grandis	not swollen	twisted but not into a helix
Tipula (Yamatotipula) furca	swollen	uncoiled
Tipula (Trichotipula) oropezoides	swollen	loosely coiled
Nephrotoma euceroides	swollen	uncoiled
Nephrotoma ferruginea	swollen	uncoiled

At the base of the semen pump and arising as an extension of the epithelium of the ejaculatory duct is a vesicular gland (Figs. 47, 50). This gland is variable in size, but it was found in all the flies studied. The muscles which move the compressor apodeme may conceal portions of this gland, and when this occurs the gland appears as if it were two glands, one at each side of the semen pump (vesicular glands, Byers, 1961). Removal of the muscles that extend from the compressor apodeme to the anterior and posterior immovable apodemes, makes possible the observation that the gland is single and surrounds the compressor apodeme in a ring-like fashion. Byers (1961) figures this gland (for the first time) as it occurs in *Dolichopeza*, in which genus it is most well developed. Here it becomes swollen into two bodies, whose shape resembles that of lima beans, one at either side of the semen pump. Byers (1961) has shown that the epithelium of this organ is composed of longitudinal bands of flattened, hexagonal cells.

Histological studies of the male reproductive system in crane flies have been made by Dufour (1851), Cholodkovsky (1905), Keuchenius (1913) and Bodenheimer (1924).

THE FEMALE REPRODUCTIVE SYSTEM

The female tipuline shows much less differentiation in the genital segments than does the male. The parts of the female associated with the reproductive apparatus, which are for the most part heavily sclerotized, are 1) the eighth sternum with its extensions, the hypovalvae, 2) the ninth tergum, 3) the ninth sternum, 4) the vaginal apodeme, 5) the tenth tergum, 6) the infra-anal plate (eleventh sternum?), and 7) the cerci. For a generalized diagram of the parts now to be considered see Fig. 59. The eighth abdominal segment shows modification only in the eighth sternum and it will be considered first.

EIGHTH STERNUM

Projecting from the distal end of the eighth sternum are the bladelike hypovalvae, which are here considered extensions of the eighth sternum that function in oviposition. They are variable, being developed and elongate, as in *Tipula (Lunatipula) triplex,* to very small or rudimentary, as in *Tipula (Vestiplex)* spp.

Rees and Ferris (1939) designate the basal area of the eighth sternum "8th sternite and coxopodite," while each hypovalve is labelled "gonapophysis of the 8th segment." They state that from the posterior dorsal angle of the eighth sternum in *Limonia sciophila,* a limoniine crane fly, there arises an elongated, bladelike lobe, the base of which is partially set off by a deep furrow from the remainder of the sternum, although there is no actual separation of the parts. They adopt the view that this lobe represents a gonapophysis (in the appendicular sense of the term). As I do not consider this structure a gonapophysis but rather a modified portion of the sternal region and because this term has had too many meanings, I have avoided the term gonapophysis. The term hypovalve has shortcomings as well. In female Diptera the hypovalve (hypogynal valve, Crampton, 1942) is defined as an appendage of the eighth sternum homologized with the gonapophysis. I have used it in order to avoid adding yet another term to the already replete terminology for this part and because the term is certainly more restricted in meaning than is gonapophysis.

Ninth Tergum

The ninth tergum undergoes no special modification in any of the flies I have studied. Rees and Ferris (1939:72, Fig. 87) figure what I believe is probably a separated piece of the ninth tergum. They called this sclerite "coxopodite."

Ninth Sternum

Directly below the ninth tergum and above the hypovalvae is a roughly triangular-shaped extension of the body wall, the ninth sternum. It is not always entirely sclerotized, and even when it is the actual limits of the sclerotized areas are not always distinct. In some flies, such as species of the genus *Dolichopeza,* a sclerotized extension from the ninth tergum runs down to meet the heavily sclerotized portions of the ninth sternum. The ninth sternum may vary in shape and size and in many instances offers good taxonomic characters. Portions of the sclerotized areas of the ninth sternum have been considered gonapophyses; again I believe this term unwarranted.

Vaginal Apodeme

The term vaginal apodeme of the female has been used by dipterists (Tuxen, 1956) for sclerotizations in the vaginal wall in Nematocera. In the literature concerning the Phlebotominae (Diptera:Psychodidae) a structure in the same general area as this apodeme has been called the furca. Byers (1961) adopted this term furca for what I recognize as the vaginal apodeme because in flies of the genus *Dolichopeza* it is forked. In many tipulines I have examined this structure is not forked. Snodgrass (1903) believed that a plate, which apparently separated from the apodeme proper in *Tipula vittata,* might represent the fused first gonapophyses, but I do not think this plate represents fused gonapophyses.

The apodeme is found in a usually membranous area of the eighth sternum caudal to the gonopore and projects into the body of the fly, where it is found lying directly above the common oviduct. It is not equipped with muscles of any sort, as far as I can tell.

Tenth and Eleventh Terga, Infra-Anal Plate (Eleventh Sternum?) and Cerci

The most conspicuous modification in the tenth segment and more specifically the tenth tergum is a median longitudinal inflection (Figs. 68, 69, 71) to which powerful muscles that move the cerci

are attached. In addition there are intersegmental muscles which take their origin from the ninth antecosta, extend through segment ten, and insert on the rim of the cercus, as well as muscles that originate on the tenth antecosta and insert on the strongly sclerotized base of the cercus. Rees and Ferris (1939) called attention to a sclerite found in *Limonia sciophila,* located posterolaterally to the tenth tergum and basal to the cercus. In that species they showed that muscles arise from the tenth antecosta and insert on this sclerite, which was thought to represent a fragmentum of the eleventh tergum.

As evidence for the supposed homology of this sclerite with a fragmentum of the eleventh tergum Rees and Ferris called attention to a similar sclerite found in *Gryllus,* which was discussed by Snodgrass (1933:70). I feel that the comparison with the gryllid is unjustified; however, the sclerite may truly represent a part of the eleventh tergum in the limoniine. Rees and Ferris stated that no such sclerite is found in *Tipula reesi*, nor did I find it present in any Tipulinae.

It is possible that the muscles which operate the cerci and arise from the tenth antecosta are true intersegmental muscles. The muscles that arise from the ninth antecosta as well as those which arise from the median longitudinal inflection of the tenth tergum may represent secondary adaptations for the operation of the cerci in oviposition. Similar secondary modifications have apparently occurred in the Japygidae (Diplura), where the muscles which operate the pincers-like cerci occupy the greater portion of the tenth abdominal segment. I am inclined to believe that in the species I have studied no true eleventh tergum is present and that only the infra-anal plate, lying directly below the anus, appearing as a flap-like appendage which is often divided into two, may represent the eleventh sternum. No sclerotized tenth sternal plate can be found in female crane flies. The membranous connection between the infra-anal plate and the ninth sternum may be thought of as the region of the tenth sternum.

The cerci arise at the apex of the tenth tergum and usually appear as strong blade-like elements but may be reduced to fleshy lobes, as in *Tipula bicornis, Tipula (Hesperotipula)* spp., and *Tipula nobilis.*

Internal Anatomy of the Female Reproductive System

The remaining parts of the female reproductive system consist of the following: 1) a pair of ovaries, 2) the common oviduct, 3) the lateral glands of the common oviduct, 4) the bursa copulatrix

and three spermathecae with their respective ducts, 5) a pair of accessory glands, and 6) the genital chamber (Figs. 42, 59, 86, 89).

Because these parts of the female genital tract bear great similarity to those of the chironomid described by Abul-Nasr (1950), I believe that in all probability they have arisen in the same fashion. There are, however, noticeable differences which must be pointed out.

Perhaps the most significant difference is the presence of the already described ninth sternum, which is well developed in the tipulid and rudimentary in the adult chironomid. No structure comparable to the "insula" (in the sense of Abul-Nasr) of the chironomid occurs. Therefore we see no flap-like evagination between the openings of the bursa copulatrix and the opening of the accessory glands when these openings are separate from each other.

Genital Chamber

If we accept Abul-Nasr's (1950) interpretation of the development of the chironomid, and if it is actually comparable to that of the tipulid, then the genital chamber of the crane fly is comparable in extent to what he has designated the atrium (vaginal and caecal portions considered as one). The genital chamber occupies the interspace between the eighth and ninth sterna. Because of the absence of "insula," no distinct division of the genital chamber into caecal (accessorial) and vaginal sections is recognized, although between the opening of the common oviduct and the openings of the bursa copulatrix and accessory glands is found the vaginal apodeme.

Accessory Glands

A pair of glands (parovaria, colleterial glands, caeca) opens from a common stalk close to the opening of the bursa copulatrix, in all of the tipulines studied, except in *Dolichopeza,* as reported by Byers (1961), where they open onto the basal portion of the bursa copulatrix. These glands assume various shapes (Figs. 75-81) in the different species studied, and their opening, which is usually a common stalk and which would be equivalent to the caecal atrium (Abul-Nasr, 1950), may be well removed from the opening of the bursa copulatrix as in *Tipula (Lunatipula) unicincta* (Fig. 60), a situation comparable to that found in *Panorpa* (Mecoptera). Usually these glands open in the intersegmental membrane between the eighth and ninth sterna; however, this membranous area may become sclerotized as in the aforementioned species (and also in *Panorpa*) and even become specialized in that it becomes swollen ventrally at the openings of the accessory glands and the bursa copulatrix (Figs. 60, 63).

BURSA COPULATRIX, SPERMATHECAL DUCTS AND SPERMATHECAE

Cephalad from the opening of the accessory glands, and occurring also in the intersegmental membrane between the eighth and ninth sterna, is the opening of the bursa copulatrix. In his 1950 paper Abul-Nasr describes what is here termed bursa copulatrix and spermathecal ducts with their terminal spermathecae, but he does not give these parts individual names. I use separate names for the various parts, although they may have a single origin.

The bursa itself is an elongate, cylindrical tube (which is lined by a cuticulum that can withstand the action of potassium hydroxide). At its anterior end it may be curved into a crook as in *Nephrotoma* (Fig. 86), or it may remain straight as in *Tipula* (Fig. 90). In *Dolichopeza* it becomes swollen at its terminus, and for this reason Byers (1961) labelled it the "functional spermatheca," the thought being that perhaps the function of sperm storage is carried out for the most part in this terminal portion.

Somewhat before the terminus of the bursa copulatrix, three slender, elongate and flexible spermathecal ducts arise and lead to balloon-like spermathecae.

OVARIES AND LATERAL OVIDUCTS

A pair of sac-like ovaries is found in the tipulid, and these seem to open directly into a common oviduct. When flies are studied in which the eggs have already been laid, one is tempted to recognize lateral oviducts in a general area where there are what appears to be attenuated ovaries. Whether there are true lateral oviducts present is hard to decide, but gross anatomical observations do not point to this.

A number of incompletely developed eggs may be found in the ovaries of females that have completed oviposition. Bodenheimer (1924) reports that in *Tipula oleracea* from 450-650 ripe eggs are laid and that from 10-30 pink colored eggs which never complete development are frequently found in females after oviposition. Byers (1961) reported that in *Dolichopeza* he could see ovaries with fully-developed eggs in females just emerged from the pupa. In the light of this evidence and the fact that the abdomens of these flies were not swollen it seems highly likely that the females which I studied that appeared to have relatively undeveloped eggs had already oviposited. Some of these females, however, were still teneral and therefore copulation and oviposition must have taken place soon after emergence from the pupa. In addition, the fact

that in crane flies usually all the eggs are deposited at once or in a short period is significant. This condition is suggested by the arrangement of the eggs, which in the tipulines studied almost completely surrounded a common lumen but which in *Dolichopeza* (Byers, 1961) are primarily in a lateral arrangement (Figs. 42, 89).

Each ovary in the specimens of *Tipula* and *Nephrotoma* I have examined ends in a single, long and tapering terminal filament. These filaments seem to extend into the thorax but I could never be sure of their final point of attachment. Bodenheimer (1924) states that they attach to the metanotum. The ovaries when replete with eggs fill the greater part of the abdomen.

Common Oviduct and Its Lateral Accessory Glands

Each ovary joins the common oviduct in the eighth abdominal segment; the common oviduct opens into the genital chamber, the gonopore being located in the membrane between the eighth sternum and the vaginal apodeme.

The common oviduct in its basal half (nearest to the gonopore) is ensheathed by a strong coat of circular muscles. In *Dolichopeza* (Byers, 1961) this ring of muscles is not strongly developed. At the base of the common oviduct there appears a pair of lateral outpocketings. To my knowledge these have not been reported in crane flies, although Potter (1938) reported similar outpocketings in Mecoptera. She called these lateral accessory glands. I could not find these outpocketings in *Dolichopeza*, but they were seen in all the other tipulines examined. Whether they are in actuality glandular is not clear. One must carefully dissect away the greater part of the muscle coat in order to see these structures. The common oviduct (Fig. 59) opens into the genital chamber at the gonopore, which is situated below the openings of the bursa copulatrix and the accessory glands.

Immediately in front of the gonopore and surrounding it on three sides is a rim-like outpocketing of the membranous portion of the eighth sternum. In addition, immediately posterior to the gonopore is a single cushionlike outpocketing of this same membrane. This cushion fits into the open side of the first outpocketing and is thus capable of closing the gonopore (Fig. 62).

It is interesting to note the similarities which exist in features of the internal anatomy of the female reproductive system of the crane fly and that of the bittacid (Mecoptera). The reproductive system in the bittacid has a pair of ovaries similar to those of *Dolichopeza*

(as figured by Byers, 1961), a set of accessory glands opening on a common stalk and separate from the opening of the bursa copulatrix as in *Tipula,* and a pair of lateral accessory glands at the base of the common oviduct; the only striking difference is the presence of but one spermatheca. The male's internal anatomy bears a striking resemblance to that of the crane fly *Dicranomyia chorea,* although the bittacid has the testes divided into four spindle-shaped sperm tubes.

NOTES ON THE HISTOLOGY OF THE FEMALE REPRODUCTIVE SYSTEM

Bauer (1933) has made a detailed study of the structure and development of the ovary of *Tipula paludosa* Meig. The important facts gleaned from this paper are here presented. The germinative cells of the larval ovary of *Tipula paludosa* are surrounded by a peritoneal sheath, a tunica propria, and the ovarial epithelium. Continuous with the ovarial epithelium are the terminal filament and the oviduct. The terminal filament is strongly developed within the body of the ovary and is derived from epithelial cells. This terminal filament is, however, not formed by the union of ovariole filaments as in the case of the grasshopper. Within the body of the ovary are found groups of oögonial cells separated from each other by small cells. Each oögonial cell divides by mitosis into sixteen cells forming groups (Eianlagen); this development goes to completion in the larval stages. Further proliferation of these cells does not take place. In the pupa an egg calyx is formed. Subsequently, the Eianlagen, which are surrounded by a follicular epithelium, become attached to this egg calyx by means of cells which form small stalks. During development, the numerous Eianlagen make random movements within the ovary and become attached to each other by small cell stalks similar to those which attach the Eianlagen to the egg calyx. For this reason one cannot say that true ovarioles are formed but rather egg chains or pseudovarioles. It can be seen from this that the eggs of any one chain do not originate from any one group of germinal cells confined within a germarium. Growth of the egg cells is accompanied by an enlargement of the nuclei. The nutritive cells do not show any increase in size. A secondary muscular sheath which envelops the ovary is derived from cells which are loosely connected, and tracheae lie appressed to the ovary and penetrate it as well. The dieroistic ovaries of *Aphidius* and of the Coccidae have nothing in common with those of the crane flies.

The following notes concerning the histology of the female re-

productive organs of *Tipula oleracea* were obtained from Bodenheimer (1924). The "Leitungsapparat" is composed of an "Eiergang" (common oviduct) and a "Vagina" (gential chamber). In the first portion of the common oviduct one finds a thin cubical epithelium surrounded by a coat of longitudinal muscle fibers, which is further surrounded by a very weak sheath of circular muscle. In the second half of the common oviduct the innermost epithelial layer becomes developed into what is described by Bodenheimer as "Zotten," or villous epithelium. This part of the common oviduct is covered by a very strong coat of circular, striated muscles. It is at this point that I have observed the lateral accessory glands, but Bodenheimer apparently did not recognize them in *Tipula oleracea*. Bodenheimer states that at the point where the common oviduct gives way to what is in this paper recognized as the genital chamber the epithelium again becomes more or less cubical and develops a chitinous intima clothed with small, thin hairs.

The ducts of the three spermathecae (receptacula seminis) join to form a common conduit the bursa copulatrix (ductus spermaticus). Each spermatheca is covered by a glandular epithelium and lined with a chitinous intima. Dufour (1851) interpreted the spermathecae as sebaceous glands (glandes sebifiques). Since these organs have been observed to become filled with sperm cells they are more properly considered receptacula. The epithelial tissue covering them is unevenly developed and is composed of columnar cells which contain large nuclei, are rich in vacuoles and are deficient in plasma. This glandular epithelium continues as a covering over the spermathecal ducts. The spermathecae are irregular in shape in *Tipula oleracea*, according to Bodenheimer; I find that they may be uniformly spherical in some other flies.

Leydig (1883), studying *Calliphora erythrocephala* (Diptera: Calliphoridae), wondered why a glandular material should be formed over a chitinized intima. He assumed, as one would have to, that there must be many pores in this intima if the glands were to serve a secretory purpose. Bodenheimer (1924) states that he could find, in the spermathecal intima, many such pores which had diameters ranging from 1-2 microns. Where the epithelium was thickest he observed the greatest number of pores, as might be expected.

The lumen of the bursa copulatrix is larger than that of the spermathecal ducts, and the chitinous intima is thicker. He states that the epithelium is thin but is raised in a ring-like band by virtue

of its nuclei which are intensively colored. It is covered by smooth circular muscle.

The accessory glands (Ectadenien, Kittdrüsen, parovaria, colleterial glands), were misinterpreted as seminal reservoirs (reservoires seminaux) by Dufour (1851). Bodenheimer states that the epithelium of these glands is composed of a flat, thin, tissue, rich in vacuoles and lacking any chitinous intima. Within may be found a slimy substance (schleimiges Gerinnsel) but never a trace of an admixture of sperm. I have no information concerning the exact function of these glands, so to call them glands is perhaps, at this point, not strictly justifiable. That they are well-developed in females of species that lay their eggs by digging into the soil with their ovipositors as well as in non-digging forms, such as *Tipula bicornis*, would suggest that they have nothing to do with lubricating the ovipositor.

My gross anatomical observations of the ovaries of species in the genera *Tipula* and *Nephrotoma* are in agreement with those of Bauer (1933). Similar observations made by Byers (1961) for *Dolichopeza* suggest the development of ovarioles in a lateral arrangement. Whether these ovarioles are developed in the same manner as those of *Tipula paludosa* cannot be stated at this point.

DISCUSSION

During this study seventy-nine species of Tipulinae were examined. Representatives of the two remaining subfamilies of Tipulidae (Limoniinae and Cylindrotominae) were examined for purposes of comparison. Conclusions drawn from this study are based almost exclusively on characteristics of the genitalia, wing venation being relied upon to some extent to provide additional supporting evidence. While the genitalia provide many good characters upon which to base a classification, sole reliance on such a complex is unwise. The correlation of additional morphological information in the adults coupled with similar data for the larvae and pupae, as well as biological studies, can lead to the best possible taxonomic treatment of any group. Despite these considerations, similarities in structure in and between various subgroupings of this subfamily can be pointed out. Table 6 indicates relationship as suggested by resemblance but should not be regarded as a phylogenetic tree. The scheme attempts to associate forms which show morphological similarities. I believe that there can be observed a gradual and general increase in complexity in the genitalia as one progresses from top to bottom of the tabulation.

Table 6.—Scheme of Relationships Based on Genitalic Characters.

Longurio; Megistocera; Brachypremna
Nephrotoma; Dolichopeza *Tipula (Trichotipula)* *Tipula (Nobilotipula); Tipula (Schummelia)*
Tipula (Nippotipula) *Ctenophora; Tanyptera; Holorusia; Prionocera; Tipula (Arctotipula)*
Tipula (Yamatotipula); Tipula (Vestiplex) *Tipula (Tipula)* *Tipula (Oreomyza) trivittata* group; *Tipula (Oreomyza) borealis* group
Tipula (Lunatipula); Tipula (Hesperotipula) *Tipula (Eumicrotipula)*

By complexity is meant deviation from a simple form (the simple form occurring more often than the complex in the flies I have studied) or one that occurs widely in the group. A few examples illustrate the presence of simple and complicated structures in the same group. In the male *Longurio* we find the basimere free from the ninth sternum, a condition that is widespread in the Limoniinae as well. On the other hand the basimere may become enveloped by the ninth sternum, as in the subgenus *Yamatotipula,* so that the point of union of these two parts cannot be observed externally. The latter form seems more specialized. The adminiculum may be an unmodified, sclerotized projection of the ninth sternum in *Yamatotipula,* whereas it becomes greatly modified in *Lunatipula,* as may be seen by comparison of *Tipula (Yamatotipula) albocaudata* with *Tipula (Lunatipula) australis.* The latter form shows in this structure "specialization," which I wish to stress is not intended to indicate a more recently evolved phenomenon, although this may in fact be the case.

Earlier in this paper discussion of the eighth sternum and ninth tergum and sternum of the male was deferred. A few words may now be said concerning these parts. Figures 25, 104 and 105 show variations in the eighth sternum. Between sterna eight and nine of males one frequently observes "lobes," which may be strongly developed (possibly functioning in copulation) and equipped with a musculature or moving by virtue of their close proximity to sclerotized plates which may also serve for the attachment of muscles. Lobes of this sort are commonly found in the subgenus *Lunatipula.* In this same subgenus one may observe other lobe-like processes,

varying in their shape and size and arising from the region of the ninth sternum. These I have called fragmenta of the ninth sternum (following Rees and Ferris, 1939). Comparison of the subgenera *Oreomyza* and *Lunatipula* suggests that such fragmenta may explain the origin of the so-called lateral appendages of the dististyle (used by taxonomists) in the *borealis* group of *Oreomyza*. Species of the *trivitatta* group of *Oreomyza* lack the lateral appendages found in those of the *borealis* group and in addition show a tendency toward reduction of the basimere. In the *borealis* group the development of these appendages seems to be correlated with complete reduction of the sclerotized body of the basimere, this area being wholly membranous except for the basal rim, to which muscles are attached. Such a reduction would seem to allow freer movement of the appendage. Furthermore, this suggests that the *borealis* group is derived from the *trivittata* group. Strong development of the fragmenta into pendant lobes is present also in the subgenus *Tipula* and can be seen in *Tipula (Tipula) pendulifera*. In this group the ninth tergum and sternum are united, suggesting a relationship to *Yamatotipula* and *Vestiplex*. The presence of fragmental lobes may represent a parallelism with the *borealis* group of *Oreomyza*.

The sternal region of the subgenera *Tipula (Yamotipula)* and *Tipula (Oreomyza)* has a strong tendency toward development of a median membranous area. In the species of *Tipula (Tipula)* I have not found this condition so far advanced.

The ninth tergum is variously modified throughout the Tipulinae; I have figured only a few variations (Figs. 123-127) in the subgenus *Yamatotipula*. Reference can be made to taxonomic works, such as those of Alexander, where the shape of the ninth tergum enables the taxonomist to identify readily many species. There is a median forked projection on the undersurface (morphologically caudal) of the ninth tergum in all three forms of *Tipula (Tipula)* examined. See Figure 18 of *Tipula spenceriana*. Presence of a tergal "saucer" at the tip of the ninth tergum is quite characteristic of the subgenus *Vestiplex* of *Tipula*. A modification of a comparable area occurs as well in species of the *borealis* group in *Tipula (Oreomyza)*, though in the latter the tip, while heavily sclerotized, is turned down, not up as in *Tipula (Vestiplex)*. In *Tipula (Vestiplex)* the basimeres are quite distinct, the median line of the ninth sternum is membranous, and the adminiculum is well-developed though simple. In the single species I examined, *fultonensis*, one may observe that the adminiculum is apparently divided medially by membrane.

Such a division has in the past led some morphologists to conclude that it represented two gonapophyses closely appressed, but such a conclusion seems unnecessary in view of the fact that the median line of the ninth sternum in so many forms has become membranous.

In the few species of limoniines examined (*Erioptera, Epiphragma, Limonia, Pedicia*) the intromittent organ is a straight, tube-like process. A similar condition exists in *Brachypremna, Megistocera* and probably also in *Longurio*, which is in other characteristics similar to *Brachypremna* and *Megistocera.* It seems highly probable that this form of intromittent organ represents the basic type in crane flies and that all other types have evolved from it. The intromittent organ of *Tipula (Nippotipula) abdominalis* is superficially similar to the one already mentioned but differs markedly in features of the aedeagus (Figure 7). I have examined only one cylindrotomine, *Phalacrocera tipulina,* as well as figures of the genitalia given by Peus (1952). In this species further modifications have taken place, such as the development of a tripartite aedeagus, but in other general aspects the intromittent organ as well as the semen pump resemble those of all the tipulines studied, with the exception of those already mentioned. In *Phalacrocera* the semen pump is not rotated dorso-caudally and therefore does not cause the arc characteristic of the aedeagus in *Tipula, Nephrotoma, Holorusia,* etc.; however, the semen pump does agree well in other aspects with these genera.

With but slight modifications of the wings in the genus *Nephrotoma* (reduction of Sc 1 and loss of Rl + 2), we can derive the wing of *Dolichopeza.* Features of the internal anatomy of the reproductive system show other similarities, including reduction in the size of the semen pump in *Nephrotoma,* with relative increase in the size of the immovable apodemes and compressor apodeme. When the semen pump is reduced in size the compressor apodeme is partially forced out and appears to lie on top of the body of the pump. This feature is common in the genus *Nephrotoma.* The compressor apodeme is cleft in the bulk of tipulines; however, it may lack a pronounced cleft in *Nephrotoma* and *Holorusia* and may show no cleft in *Dolichopeza.* Intermediate forms occur in *Dolichopeza* and *Nephrotoma.*

Running cephalad from the adminiculum of *Dolichopeza* there are two well-developed sclerotizations in the genital sac (adminicular rods, Byers, 1961) which extend to the semen pump and which act as a fulcrum for its rotational movement. In this genus the

sclerotizations are quite pronounced. I have found similar sclerotizations in *Nephrotoma* (*ferruginea, euceroides*), but they are by no means as well developed and are visible only as faint longitudinal lines, quite easily overlooked.

Characteristic of *Dolichopeza carolus, venosa,* and *subvenosa* is the development of an intromittent organ of large bore. In *Nephrotoma* the exact opposite has occurred, this organ frequently appearing attenuated and much lengthened. It may extend far into the abdominal cavity causing the genital sac to become correspondingly lengthened. In *Nephrotoma ferruginea* it extends to the anterior margin of the fifth abdominal segment where it then bends caudally in a small arc and runs caudally to its point of emergence. This elongation of the intromittent organ seems characteristic of the genus as a whole; however, it occurs also in other species (*Tipula bicornis, Tipula macrophallus*).

In this connection there is an interesting similarity between *Tipula (Trichotipula) macrophallus* and the genus *Nephrotoma.* The species was described by Dietz, who placed it in *Pachyrrhina* (now *Nephrotoma*). Although it can now be shown to fall within the genus *Tipula,* subgenus *Trichotipula,* its internal anatomy suggests a close relationship to *Nephrotoma.* Other workers have in the past considered *Trichotipula* to be very closely related to *Nephrotoma.* The intromittent organ is developed in a way identical to that of *Nephrotoma* and its length exceeds that of this part in any species of *Nephrotoma* I have examined, extending well into the thorax before turning caudad. The bursa copulatrix in the female of this species is proportionately long.

Tipula (Nobilotipula) nobilis possesses a robust intromittent organ similar to that found in *Dolichopeza carolus, venosa,* and *subvenosa* and in addition has sclerotizations in the genital sac which run cephalad from the adminiculum to the semen pump. The telomeres of *nobilis* are like those of *Dolichopeza.*

Among the species studied in the genus *Nephrotoma* were seen two distinct lines of modification of sternal and basimeral areas. In *Nephrotoma ferruginea* the basimere is not reduced in size, in comparison with other Nephrotomas, and the tergum and sternum extend approximately the same distance from their respective antecostae. Lines possibly radiating from this stem are as follows: 1) the sternum is extended caudally while the basimere is reduced in size, as in *Nephrotoma euceroides* and *polymera;* 2) the sternal region becomes uptilted while the basimere is reduced in size, as

in *Nephrotoma lugens* and *erythrophrys*. The adminicula in *Nephrotoma euceroides* and *polymera* bear a great resemblance to each other, and this too may indicate a group characteristic.

A form resembling the supposed prototype occurs in *Nephrotoma macrocera, virescens, punctum, xanthostigma,* and *breviorcornis*. Even in these species one can detect the beginnings of sternal enlargement, but these species do not fit in either of the two supposed derived groups on the basis of this feature.

Tipula (Trichotipula) oropezoides, as the name implies, resembles the subgenus *Oropeza* of the genus *Dolichopeza*. In addition to their over-all similarity there is a resemblance in the possession of lobelike appendages at the level of the adminiculum. There is a strong resemblance in the adminicula of *Tipula oropezoides* and *Nephrotoma xanthostigma*.

In the subgenus *Schummelia* I have been able to examine *T. hermannia*. This species resembles *Dolichopeza* in the development of short lobe-like evaginations of the ninth sternum (gonapophyses, Byers, 1961) on either side of the adminiculum. The genital sac possesses the longitudinal sclerotizations as are found in *Dolichopeza*. The supportive sclerite of the semen pump arising from the posterior immovable apodemes is well developed, a condition seen in *Nephrotoma* as well. In *Tipula hermannia* the semen pump and associated apodemes are quite distinct, and there is a median cephalic inflection and fusion of the posterior immovable apodemes in a fashion not observed in any other tipuline.

The reproductive structures in the genera *Holorusia, Ctenophora, Tanyptera, Prionocera,* and the subgenus *Arctotipula* of *Tipula* appear quite similar, as shown by the telomeres, the simplicity of the adminiculum, the absence of fragmenta, and the lack of median weakness in the ninth sternum such as is found in *Tipula (Yamatotipula)*. In the species examined in these groups there is partial fusion of basimere and sternum. *Tanyptera topazina* has the ninth sternum inflected in the midline causing the otherwise unmodified adminiculum to be pushed cephalad. In *Ctenophora apicata* a portion of the ninth sternum is produced caudad without causing any resulting displacement of the adminiculum.

It is difficult to place *Nippotipula* in the scheme. *Tipula (Nippotipula) abdominalis* is a most uncomplicated form as regards its external morphology. It lacks specialization of the sternum and possesses unmodified telomeres; in fact the telomeres are perhaps the least modified of all species examined. It seems to be compara-

ble to forms such as *Ctenophora*, but any further comments would be highly speculative. Most outstanding are its distinctive semen pump and intromittent organ (Fig. 7).

Yamatotipula and *Vestiplex* are placed near each other primarily because they lack a separation between the ninth tergum and sternum. Both groups show membranization in the midline of the ninth sternum but this is more pronounced in *Yamatotipula*. Loss of median sclerotization of the ninth sternum is observed also in *Tipula (Oreomyza)*, and in addition an uptilting of the ninth segment has occurred. A similar uptilting of the ninth sternum is found in *Yamatotipula*. The development of lateral appendages of the inner telomere, characteristic of the *borealis* group of the subgenus *Oreomyza*, has already been discussed. The ninth tergum and sternum remain divided in *Oreomyza*. Earlier, reasons were given for placing *Tipula (Tipula)* close to *Tipula (Oreomyza)* on the basis of the development of lateral telomeral appendages. *Tipula (Tipula)* is like *Yamotipula* in having no visible separation of ninth tergum and sternum.

Concerning the last three groups in the scheme the greatest resemblances occur between *Tipula (Lunatipula)* and *Tipula (Hesperotipula)*. Females of the *bicornis* group of *Lunatipula* and those of *Hesperotipula* are remarkably similar, both showing reduction in the ovipositor (cerci and hypovalvae). In addition the males resemble each other in the possession of appendages arising from the intersegmental membrane between the eighth and ninth sterna as well as in fragmental development of the ninth sternum. Males of *Hesperotipula* are further modified in the reduction of the ninth tergum and in the possession of elongate processes arising from the basimere. One can see the beginnings of such basimeral development in the *bicornis* group of *Lunatipula* as well. The ninth tergum and sternum are separate in both groups.

The presence of fragmenta in the ninth sternum in the species of *Lunatipula* has enabled me, so far, to recognize all species in this subgenus on sight by this character alone. Diversity in the shape of the adminiculum reaches its extreme in *Lunatipula*, as is readily seen by examining, for example, such species as *Tipula australis*, *mohavensis*, and *bicornis*.

The reasons for placing *Tipula (Eumicrotipula)* close to *Tipula (Lunatipula)* are the form of the telomeres and the development of the adminiculum. I have been able to examine only a single species of *Eumicrotipula*, *T. chiricahuensis*, and find no other out-

standing resemblances between this species of *Eumicrotipula* and those of *Lunatipula*.

It is hoped that the figures accompanying this text can clarify, to some extent, the information presented. No attempt has been made to illustrate all the species studied, and only partial drawings are given in many cases. The prime purpose of these figures is to enable the reader to locate the characters so that personal observation is facilitated. It is a difficult task to describe characters as diverse in form as are found in the tipulid terminalia, even more difficult to devise groupings on the basis of these characters. I have put down only my impressions. Finally, I wish to say that there is no better way of understanding these features than by personal observation.

SUMMARY

A gross morphological study was made of the reproductive system of 79 North American species of crane flies in the subfamily Tipulinae. Some representatives of the two remaining subfamilies were examined for comparative data. The major results obtained are as follows:

The Male Reproductive System

1. Although the main reproductive organs are on the ninth segment, the eighth is sometimes provided with structures presumably of importance in copulation.

2. The development of the intromittent organ and clasping organs in crane flies seems best explained by the phallic lobe theory, as discussed by Snodgrass (1957). Since gross dissection cannot shed light upon the mode of development of the intromittent organ, two alternative and flexible sets of terminology for the parts of this organ are offered.

3. Evidence of torsion in the terminal abdominal segments of males in the genera *Brachypremna* and *Megistocera* is reported.

4. The semen pumping mechanism is probably derived from proximal elements of the intromittent organ.

5. Two sets of immovable apodemes, which serve as points of attachment for the muscles of a movable apodeme, the compressor apodeme of the semen pump, are derived from the dorsal wall of the genital chamber.

6. The working mechanism of the semen pump and the movement of the intromittent organ are explained by operation of five sets of muscles associated with these parts.

7. The remainder of the male genital tract is composed of a pair of testes, a pair of separate vasa deferentia, a seminal vesicle, a pair of accessory glands originating at the semial vesicle, a single ejaculatory duct and a large "gland" at the end of the ejaculatory duct where it joins the semen pump.

8. The distribution of muscles to the telomeres does not require an appendicular origin of these structures. While it is impossible by the methods used to decide this point, the author prefers a sternal interpretation of these parts.

9. Three types of relationship between the semen pump and the intromittent organ were observed: a) intromittent organ a straight tube arising directly from the semen pump, b) intromittent organ bowed due to dorsocaudal rotation of the pumping mechanism (semen pump), resulting in the semen pump being dorsal to the intromittent organ, c) intromittent organ essentially straight but with a slight ventral bowing and with a peculiar enlargement of the aedeagus.

THE FEMALE REPRODUCTIVE SYSTEM

1. The segments involved in the female reproductive system are eight through eleven.

2. The functional ovipositor is derived from the cerci and the hypovalvae.

3. The eleventh tergum in female adult Tipulinae is apparently lost; the hypovalvae are thought to be extensions of the eighth sternum.

4. An infra-anal plate may represent the eleventh sternum.

5. A well-developed tenth tergum is present; however, the tenth sternum has apparently been reduced to a membranous area between the ninth sternum and the infra-anal plate.

6. The ninth sternum varies in degree of sclerotization as well as in shape; it is found directly above the eighth sternum and below the level of the infra-anal plate.

7. The vaginal apodeme, a sclerite which is inflected into the body, lies between the eighth and ninth sterna.

8. The remainder of the female genital tract is composed of a pair of ovaries with their terminal filaments, a common oviduct, a pair of lateral "glands" at the distal end of the common oviduct, the bursa copulatrix, opening on the intersegmental membrane between the eighth and ninth sterna, with three spermathecal ducts terminating in bulb-like spermathecae, and a pair of accessory glands usually

opening on a common stalk caudal to the bursa copulatrix, though sometimes directly into the bursa copulatrix. The opening of the accessory glands is located on the intersegmental membrane between the eighth and ninth sterna.

Intra- and Extralimital Relationships

1. Previously, similarities in the external anatomy of the female reproductive structures of Tipulidae and Mecoptera have been observed (Byers, 1954); the internal organs of these two groups likewise are shown to bear striking resemblances.

2. A grouping of the various genera and subgenera, based on similarities in structure and degree of complexity, of features of the reproductive system and wing venation is given, but no claim is made for the phylogenetic significance of these groups.

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PLATE I

FIG. 1.—Dorsal view of semen pump and associated parts in *Tipula (N.) abdominalis,* male. Note the enlarged club-shaped specialization of the aedeagus. AIA = anterior immovable apodeme (anteriorly divided); CA = compressor apodeme; SP = semen pump (bulb); ?PIA = though muscles could not be studied due to the fact that only dry museum specimens were available, this part may represent the posterior immovable apodeme; GS = genital sac; Ae = aedeagus.

FIG. 2.—Dorsal view of semen pump and associated parts in *Tipula (E.) chiricahuensis,* male. scl = sclerotization in dorsal wall of genital sac (epimere, Rees and Ferris, 1939).

FIG. 3.—Lateral view at apex of intromittent organ in *Tipula (E.) chiricahuensis,* male.

FIG. 4.—Arm of compressor apodeme in *Tipula (E.) chiricahuensis,* male.

FIG. 5.—Caudal view of semen pump and associated parts in *Holorusia (H.) grandis,* male. s = small supportive sclerite of the ejaculatory duct.

FIG. 6.—Caudal view of ninth segment, semen pump and associated parts in *Brachypremna dispellens,* male. Note: 1) rotation of segment nine. A = adminiculum; ED = ejaculatory duct; B = basimere; T = telomere.

FIG. 7.—Lateral view of semen pump and associated parts in *Tipula (Nippotipula) abdominalis,* male.

FIG. 8.—Caudal view of adminiculum and intromittent organ in *Tipula (E.) chiricahuensis,* male. Note complexity of adminiculum.

PLATE I

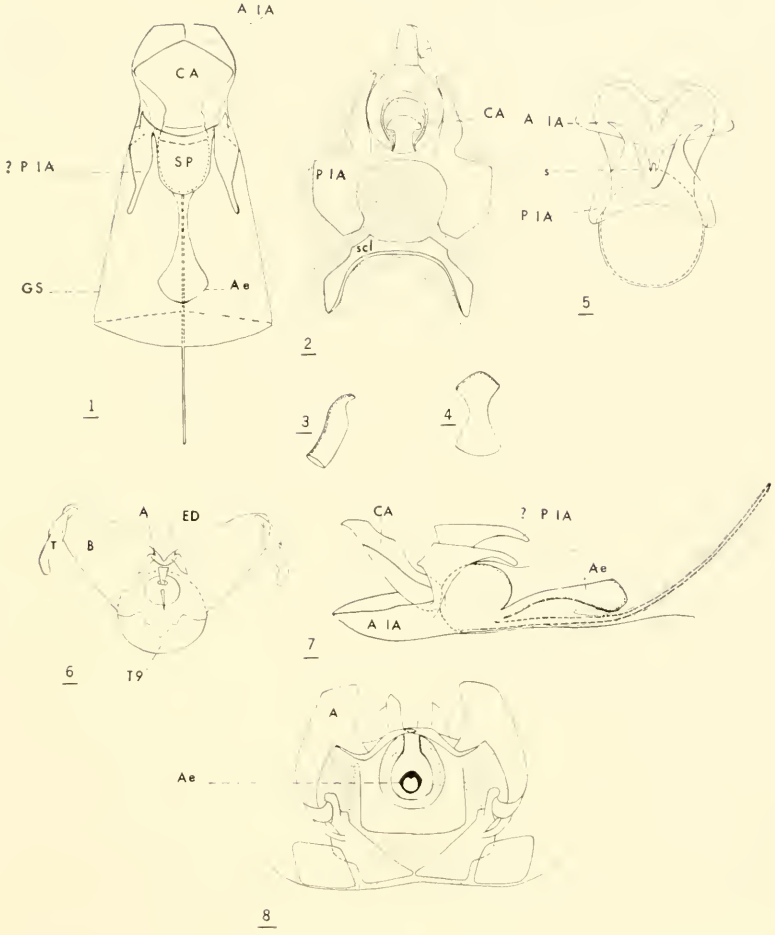
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PLATE II

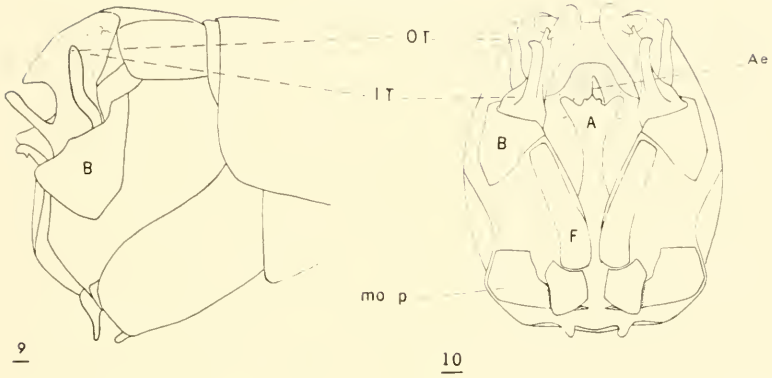
FIG. 9.—Lateral view of terminal abdominal segments in *Tipula (L.) triplex*, male. B = basimere; OT = outer telomere; IT = inner telomere.

FIG. 10.—Caudal view of *Tipula (L.) triplex*, male. A = adminiculum; Ae = aedeagus; F = fragmentum; mop = movable process of intersegmental membrane between eighth and ninth sterna.

FIG. 11.—Caudal view of ninth abdominal segment in *Ctenophora (T.) topazina*, male.

FIG. 12.—Caudal view of terminal abdominal segments in *Tipula (Nippotipula) abdominalis*, male.

PLATE II



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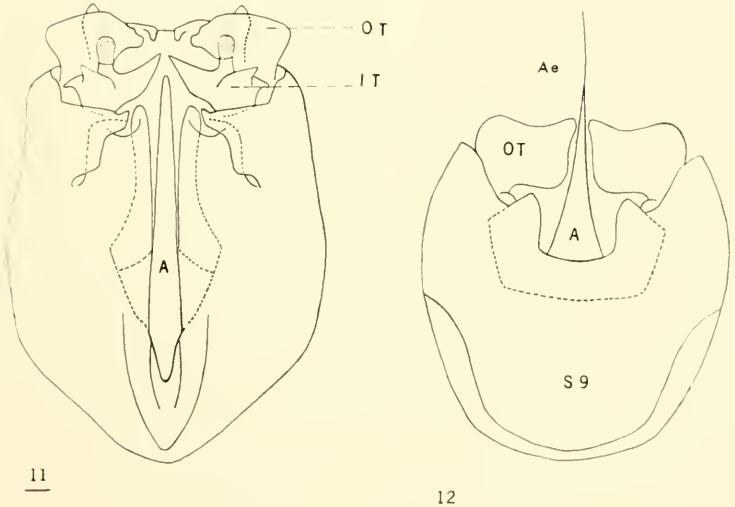

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PLATE III

FIG. 13.—Lateral view of terminal abdominal segments in *Nephrotoma cuccroides,* male, telomeres removed. Note extension of ninth sternum and development of adminiculum. A = adminiculum; B = basimere; m = an outpocketing at base of median membranization of ninth sternum.

FIG. 14.—Caudal view of terminal abdominal segments in *Nephrotoma cuccroides,* male. OT = outer telomere; m = median membranization of ninth sternum.

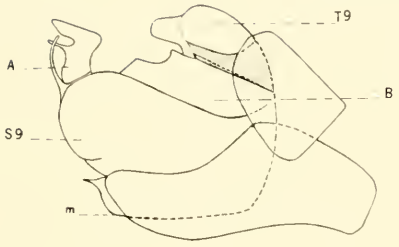
FIG. 15.—Lateral view of terminal abdominal segments in *Nephrotoma ferruginea,* male. m = base of median membranization of ninth sternum; IT = inner telomere.

FIG. 16.—Caudal view of ninth abdominal segment in *Nephrotoma ferruginea,* male, telomeres removed.

FIG. 17.—Caudal view of ninth abdominal segment in *Nephrotoma lugens,* male, telomeres removed. Note upturning of ninth sternum and fusion of tergal and sternal antecostae (an) into a single process.

FIG. 18.—Caudal view of ninth abdominal segment in *Tipula (T.) spenceriana,* male. Note median, apically divided process (mp) of ninth tergum, general membranization (m), and specialization of ninth sternum: sclerotized processes.

PLATE III



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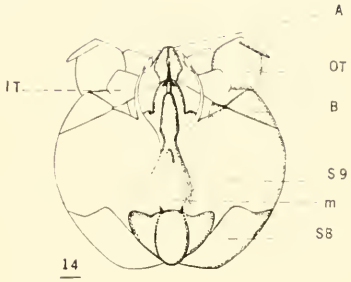

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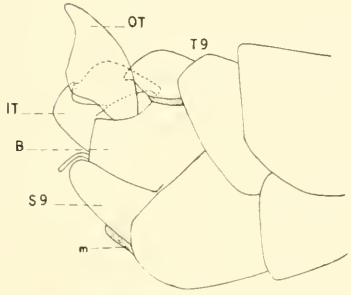

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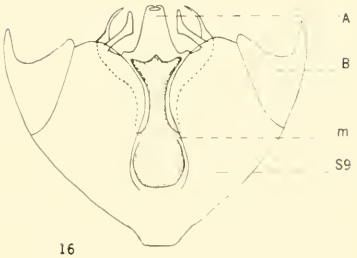

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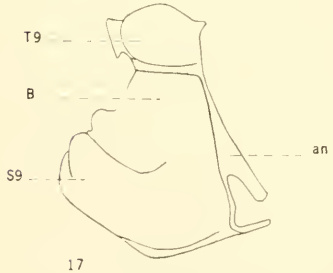

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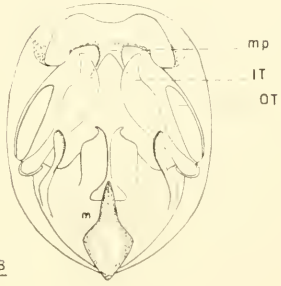

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PLATE IV

FIG. 19.—Caudal view of ninth abdominal segment in *Tipula (Y.) albocaudata,* male. m = median membranization of ninth sternum; A = adminiculum; OT = outer telomere; IT = inner telomere.

FIG. 20.—Caudal view of ninth abdominal segment in *Prionocera oregonica,* male.

FIG. 21.—Lateral view of terminal abdominal segments in *Tipula (Y.) furca,* male.

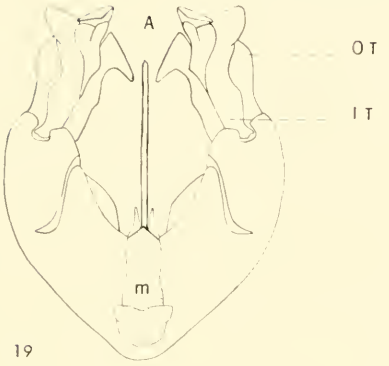
FIG. 22.—Caudal view of ninth abdominal segment in *Tipula (Y.) sulphurea,* male, telomeres removed. Note tripartite adminiculum (A) with lateral arms free.

FIG. 23.—Caudal view of ninth segment in *Tipula (Y.) furca,* male. Note extent of membranization of ninth sternum (m). Ae = aedeagus; la = lateral arm of adminiculum.

FIG. 24.—Caudal view of intersegmental lobes in membrane between eight and ninth sterna of *Tipula (L.) australis,* male. Note sclerotized plate between these lobes.

FIG. 25.—Caudal view of eighth abdominal sternum in *Tipula (L.) australis,* male, showing development of a pair of lobes.

PLATE IV



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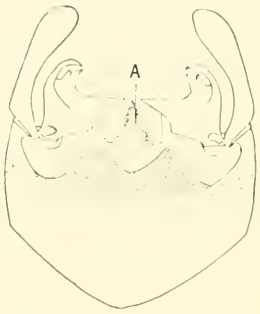

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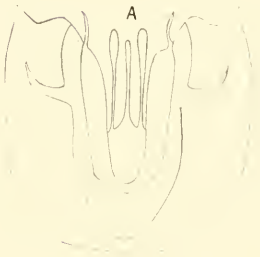

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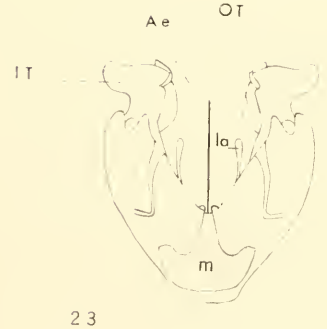

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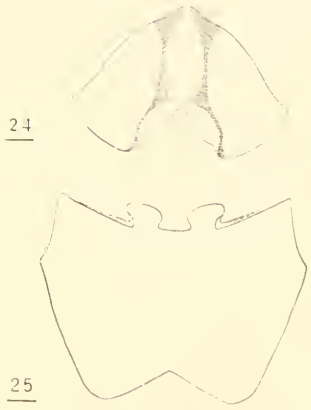

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PLATE V

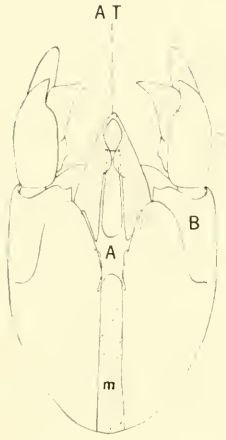
FIG. 26.—Caudal view of ninth abdominal segment in *Tipula (Y.) jacobus*, male. AT = membranous anal tubercle (= ?10th and 11th segments); A = adminiculum; m = median membranization of the ninth sternum; B = basimere; OT = outer telomere; IT = inner telomere.

FIG. 27.—Lateral view of terminal abdominal segments in *Tipula (O.) trivittata*, male.

FIG. 28.—Caudal view of ninth abdominal segment in *Tipula (O.) borealis*, male. Note development of large appendage (LA) contiguous with inner telomere.

FIG. 29.—Caudal view of ninth abdominal segment in *Tipula (O.) borealis*, male. Note upturning of ninth abdominal segment and reduction of basimere to membrane (B).

PLATE V



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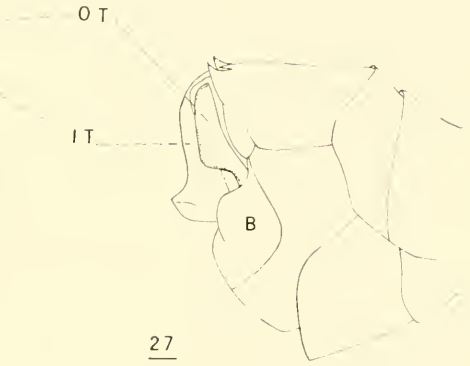

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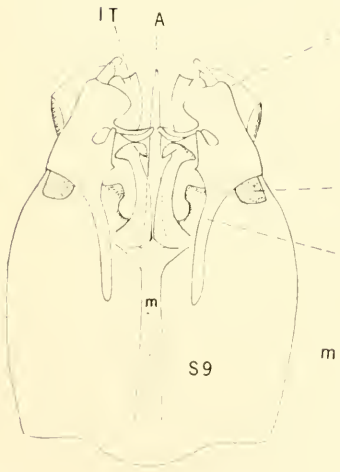

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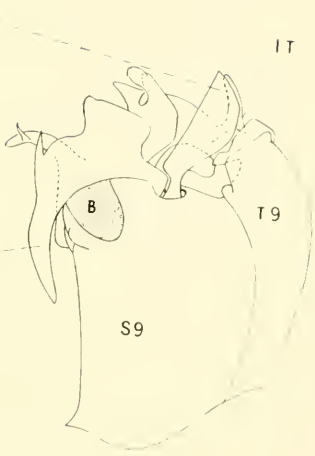

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PLATE VI

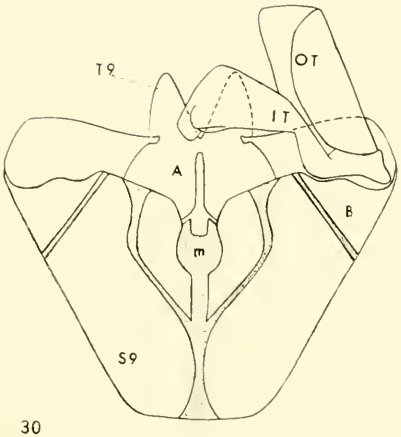
FIG. 30.—Caudal view of ninth abdominal segment of *Holorusia (H.) grandis,* male left telomeres removed. OT = outer telomere; IT = inner telomere; B = basimere; A = adminiculum; m = median membranization of ninth sternum.

FIG. 31.—Dorsal view (somewhat oblique) of ninth segment in *Tipula (H.) trypetophora,* male. Note fusion of inner and outer telomeres, reduction in size of ninth tergum, and development of basimere (B) into a long process.

FIG. 32.—Caudal view of terminal segments of *Tipula (Nobilotipula) nobilis,* female. Note reduction of cerci into small lobes, reduction of sclerotization in ninth segment leaving only two sclerotic bars; openings between "bars" of ninth sternum are of bursa copulatrix and accessory glands; opening to rear of vaginal apodeme (VA) is of gonopore (Go). IP = infra-anal plate; H = hypovalve.

FIG. 33.—Lateral view of *Tipula (Nobilotipula) nobilis,* female.

PLATE VI



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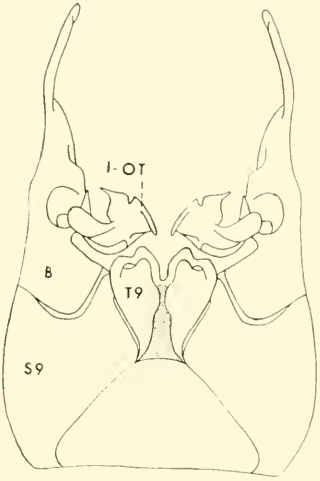

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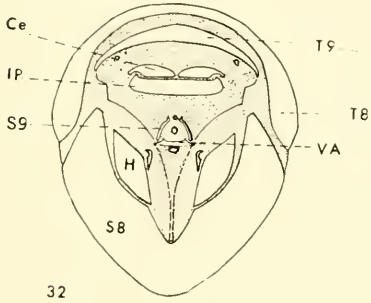

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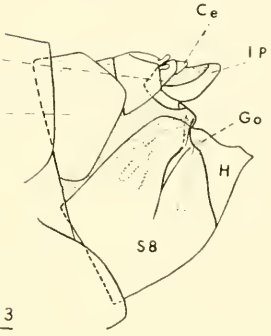

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PLATE VII

FIG. 34.—Lateral view of ninth abdominal segment of *Tipula (Y.) spernax*, male. OT = outer telomere; IT = inner telomere.

FIG. 35.—Lateral view of ninth segment of *Tipula (T.) pendulifera*, male. Note fusion of ninth tergum and sternum, pendulous lobe or fragmentum (F). B = basimere; T-S9 = fused tergum and sternum of segment nine.

FIG. 36.—Caudal view of ninth segment of *Tipula (Y.) spernax*, male.

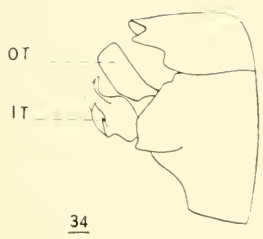
FIG. 37.—Caudal view of terminal abdominal segments of *Tipula (O.) pseudotruncorum*, male, telomeres removed. m = median membranization of the ninth sternum.

FIG. 38.—Lateral view of *Tipula (A.) semidea*, male. (Redrawn from Alexander, 1954). Note simplicity of telomeres and basimere partially fused with sternum.

FIG. 39.—Oblique ventral view of caudal abdominal segments of *Tipula (A.) plutonis absaroka*, male.

FIG. 40.—Ventral view of the ninth abdominal segment of *Tipula (A.) semidea*, male. (Redrawn from Alexander, 1954.)

PLATE VII



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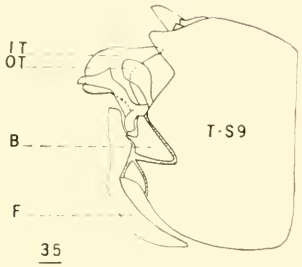

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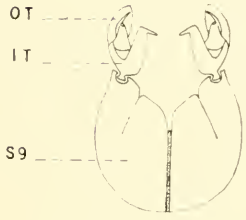

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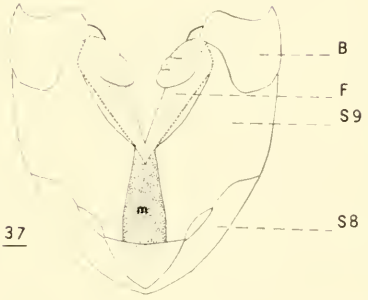

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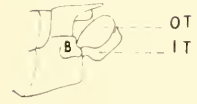

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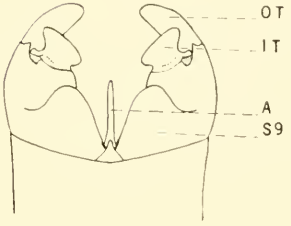

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PLATE VIII

FIG. 41.—Lateral view of *Dolichopeza (O.) venosa,* male (from Byers, 1961), to show position of semen pump and intromittent organ at rest. sGS = sclerotizations (adminicular rods) of genital sac contiguous with adminiculum (A); p = sternal process (gonapophysis); AIA = anterior immovable apodeme; PIA = posterior immovable apodeme; CA = compressor apodeme; SP = semen pump; Enph = endophallus. Only heavily sclerotized areas are shown in the figure, hence the genital sac is not figured.

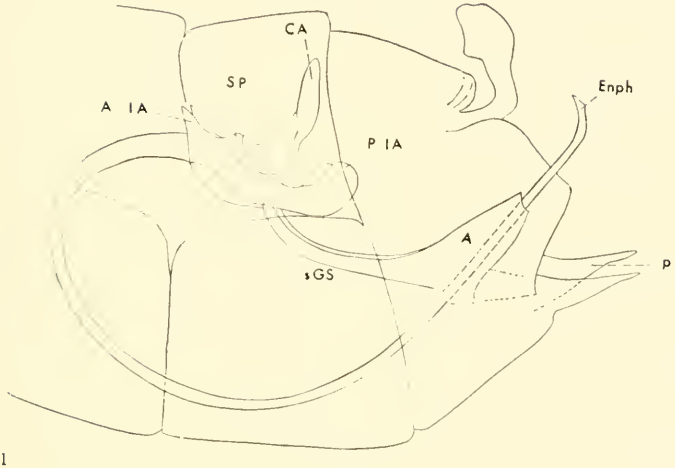
FIG. 42.—Schematic drawing to show internal reproductive features of *Dolichopeza (O.) tridenticulata,* female (from Byers, 1961). spt = spermatheca; dspt = spermathecal duct; fspt = functional spermatheca; bc = bursa copulatrix; abc = aperture of bursa copulatrix; rct = rectum; cr = cercus; acg = accessory glands; gp = gonopore; hv = hypovalve; ovl = ovariole; lov = lateral oviduct; mov = median oviduct.

FIG. 43.—Partial drawings of bursa copulatrix showing connection of accessory glands in *Dolichopeza (O.) carolus,* female. Note: 1) spermathecal ducts cut. (From Byers, 1961.)

FIG. 44.—Bursa copulatrix, spermathecal ducts, spermathecae and accessory glands in *Dolichopeza (D.) americana.* (From Byers, 1961.)

FIG. 45.—Detail of accessory glands showing their attachment point to bursa couplatrix in *Dolichopeza.*

PLATE VIII



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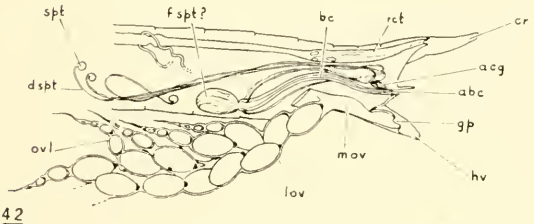

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PLATE IX

FIG. 46.—Cephalic view of semen pump in *Tipula (L.) triplex*, male, showing the relative position of sclerite (scl) ("epimere") in dorsal wall of genital sac. PIA = posterior immovable apodeme; CA = compressor apodeme; b = bulb of the semen pump; AIA = anterior immovable apodeme; Enph = endophallus.

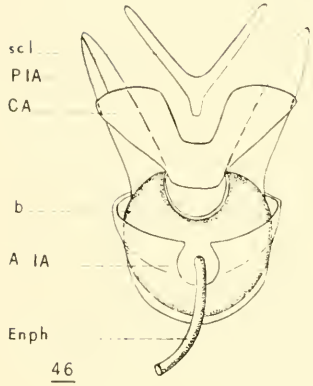
FIG. 47.—Cephalic view of semen pump of *Tipula (L.) triplex*, male showing position of the gland (G) at the base of the ejaculatory duct (ED).

FIG. 48.—Dorsal view of semen pump of *Nephrotoma ferruginea*, male. s = sclerotized brace of the semen pump.

FIG. 49.—Oblique lateral view of terminal abdominal segments of *Tipula (Nippotipula) abdominalis*, male. AT = anal tubercle; sA = sclerites associated with anal tubercle (two dorso-lateral and two latero-ventral sclerites).

FIG. 50.—Detail of gland (G) at the base of the ejaculatory duct (ED). Note sclerotized intima at the base of ejaculatory duct indicated by "ringed" tube.

PLATE IX



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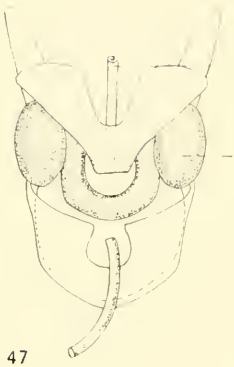

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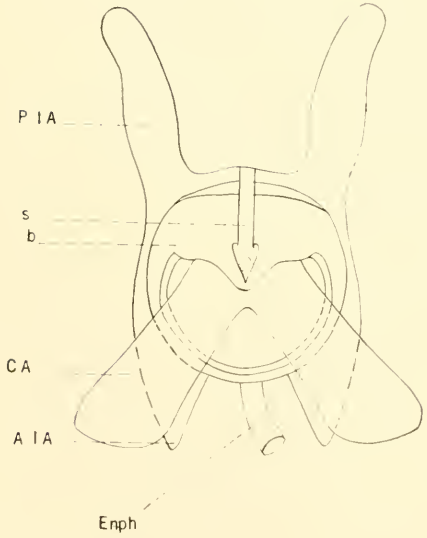

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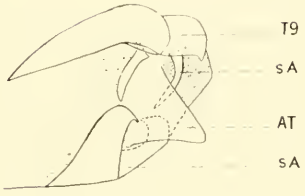

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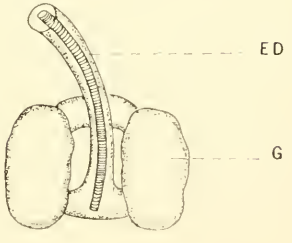

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PLATE X

FIG. 51.—Dorsal view of semen pump and intromittent organ of *Brachypremna dispellens,* male. *In situ* these structures are rotated about 180° in longitudinal plane. CA = compressor apodeme; ED = ejaculatory duct; s = supportive sclerite of the ejaculatory duct; GS = genital sac; Ae =aedeagus; Enph = endophallus.

FIG. 52.—Lateral view of semen pump and intromittent organ of *Brachypremma dispellens,* male. AIA = anterior immovable apodeme; ED = ejaculatory duct.

FIG. 53.—Lateral view of semen pump of *Nephrotoma ferruginea,* male. S_1 = semen pump brace; s = supportive sclerite of the ejaculatory duct.

FIG. 54.—Lateral view of the telomeres of *Tipula (O.) latipennis,* male. Note pendulous lateral lobe (LA) of the inner telomere (IT), and membranization of the basimere (B). OT = outer telomere.

PLATE X

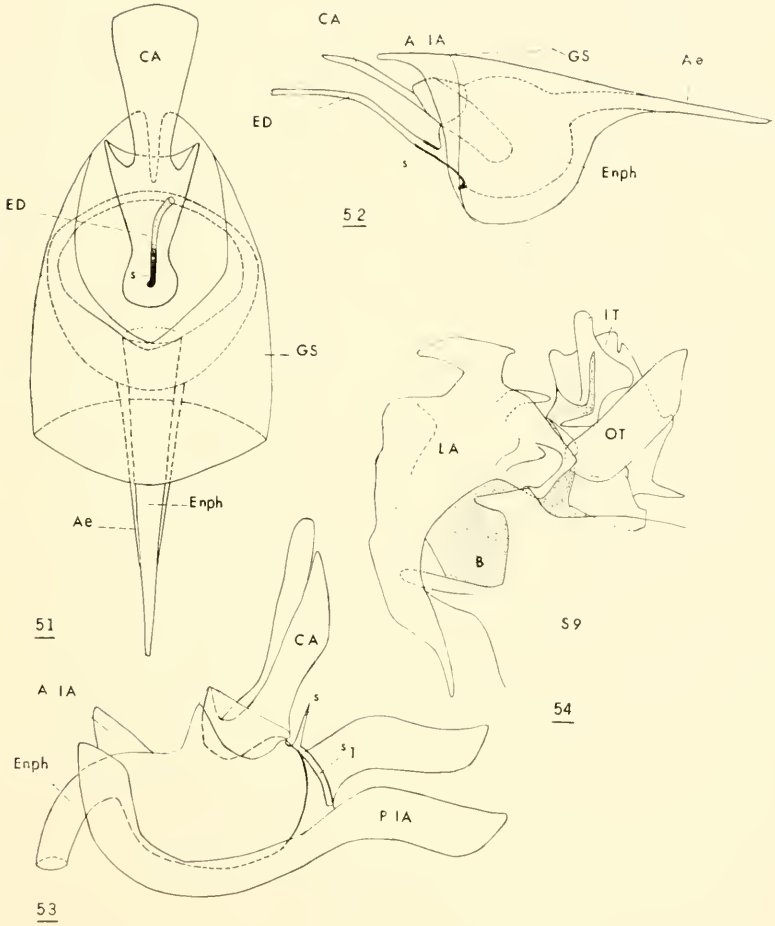
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PLATE XI

FIG. 55.—Gross internal features of male reproductive system of *Dolichopeza*. Total length of accessory glands not figured; dotted line along vasa deferentia indicates unfused but closely appressed tubes; glands at base of ejaculatory duct not figured. TS = testes; VD = vas deferens; AG = accessory glands; SV = seminal vesicle; ED = ejaculatory duct.

FIG. 56.—Gross internal features of male reproductive system. Note slight swelling of vas deferens. Dotted line along vasa deferentia indicates unfused but closely appressed vasa deferentia; glands at base of ejaculatory duct not figured.

FIG. 57.—Schematic drawing of transverse section through seminal vesicle anterior to openings of accessory glands and vasa deferentia. Note close appression of vasa deferentia which are surrounded by a tunic (tunica adipo membranacea, Keuchenius, 1913), not labelled in figure.

FIG. 58.—Semi-diagrammatic lateral view of seminal vesicle showing attachment of accessory glands (AG), vasa deferentia (VD) and ejaculatory duct (ED).

PLATE XI

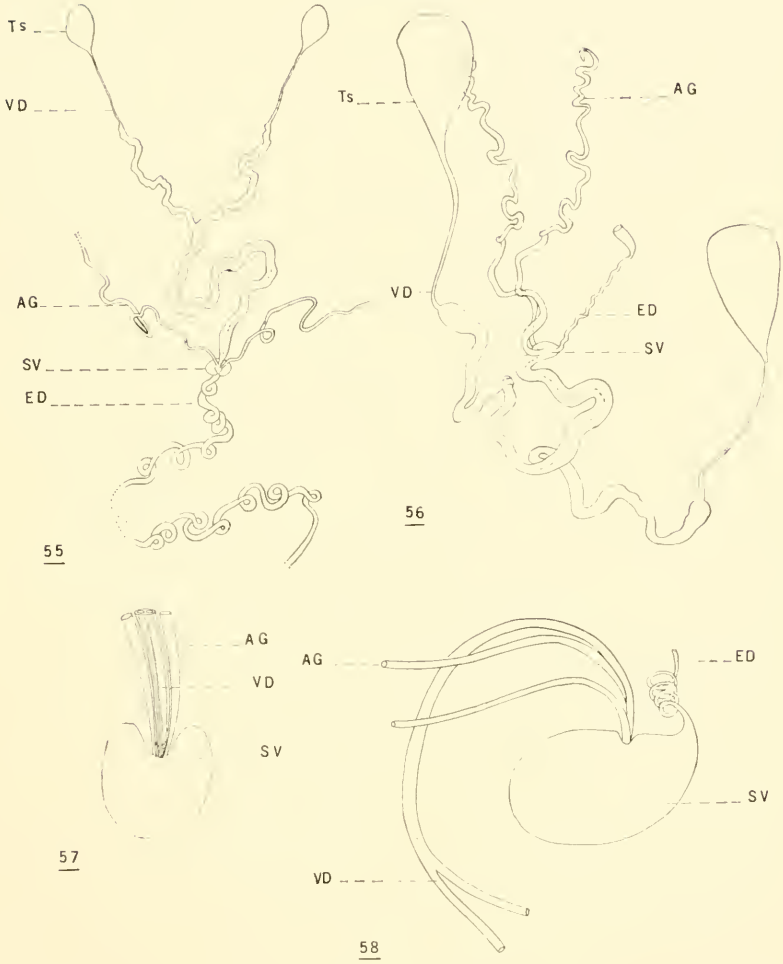

PLATE XII

FIG. 59.—Schematic drawing of terminal abdominal segments of a female tipuline. O = ovary; Sp = spermatheca; T10 = tenth tergum; BC = bursa copulatrix; VA = vaginal apodeme; LAG = lateral accessory glands of common oviduct; CO = common oviduct; Ce = cercus; IP = infra-anal plate; AG = accessory glands; H = hypovalve.

FIG. 60.—Lateral view of ninth sternum and part of eighth at opening of common oviduct in *Tipula (L.) unicincta*, female. Note development of ninth sternum at opening of accessory glands (AG) and at opening of bursa copulatrix (BC).

FIG. 61.—Sclerotization in dorsal wall of genital chamber (epimere) of *Tipula (L.) unicincta*, male.

FIGS. 62 and 63.—Diagrammatic representations of genital chamber and associated parts in *Tipula (L.) unicincta*, female. These two figures are to be used together. In Fig. 62 the openings of the accessory glands, bursa copulatrix and common oviduct are not figured; the openings have been omitted since they are not seen without manipulation of the parts, though the general area is indicated by dotted lines; the accessory glands as well as the bursa copulatrix open on a lobe; the gonopore lies between two padlike evaginations, one fitting into the other and closing the gonopore when this occurs. Go = gonopore.

PLATE XII

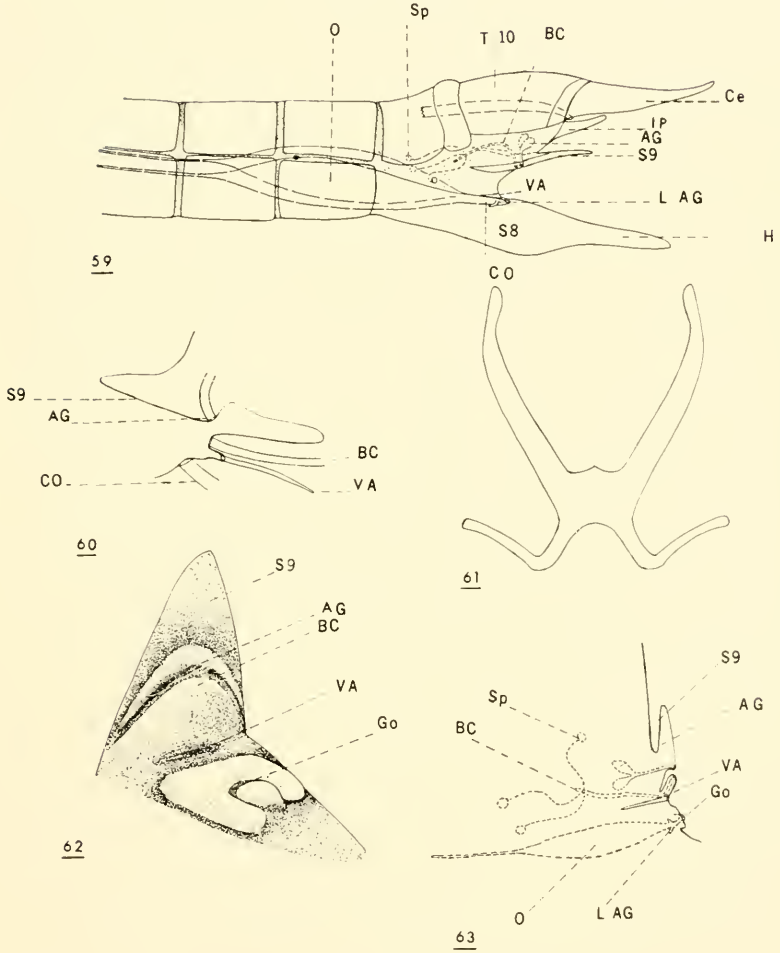
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PLATE XIII

FIG. 64.—Ventral view of eighth sternum and hypovalve of *Tipula (Y.) sulphurea*, female.

FIG. 65.—Dorsal view of tenth tergum and cerci of *Tipula (Y.) sulphurea*, female. Dotted line indicates outline of infra-anal plate.

FIG. 66.—Ventral view of eighth sternum and hypovalvae of *Tipula (Y.) spernax*, female.

FIG. 67.—Dorsal view of tenth tergum and cerci of *Tipula (Y.) spernax*, female. Dotted line shows outline of infra-anal plate, which is divided.

FIG. 68.—Ventral view of ninth and tenth terga and cerci of *Tipula (L.) unicincta*, female, showing musculature. a = muscle from ninth tergal antecosta to antecosta of tergum ten; b = muscle from ninth tergal antecosta to basal rim of cercus; c = muscle from tenth tergal antecosta to basal rim of cercus; Ap = median longitudinal apodemal inflection of tenth tergum. Muscles closely associated with those labelled (c) originate from the median longitudinal apodemal inflection. (See Fig. 69, where they are distinctly separated and labelled d.)

FIG. 69.—Ventral view of ninth and tenth terga and cerci of *Tipula (L.) triplex*, female, showing musculature. a = muscle from ninth tergal antecosta to tenth tergal antecosta; b = medially-directed muscle from ninth tergal antecosta to tenth tergal antecosta; c = muscle from tenth tergal antecosa to basal rim of cercus; d = muscle from median longitudinal apodemal inflection of tenth tergum to basal rim of cercus; e = muscle from ninth tergal antecosta to basal rim of cercus; CE = cercus. Whereas in Fig. 68 muscle (c) was singular with two points of origin, *i. e.*, from the tenth tergal antecosta and from the longitudinal median apodemal inflection, in *triplex* this muscle is separated into two muscle groups (c) and (d).

FIG. 70—Ventral view of ninth and tenth terga, bifid infra-anal plate and cerci of *Tipula (L.) triplex*, female.

FIG. 71.—Dorsal view of ninth and tenth terga and cerci of *Tipula (L.) triplex*, female.

FIG. 72.—Dorsal view of eighth sternum and hypovalvae of *Tipula (L.) triplex*, female.

FIG. 73.—Ventral view of seventh and eighth sterna and hypovalvae of *Tipula (L.) triplex*, female.

FIG. 74.—Ventral view of tenth tergum showing divided infra-anal plate (IP) below and caudal cerci of *Tipula (O.) latipennis*, female.

PLATE XIII

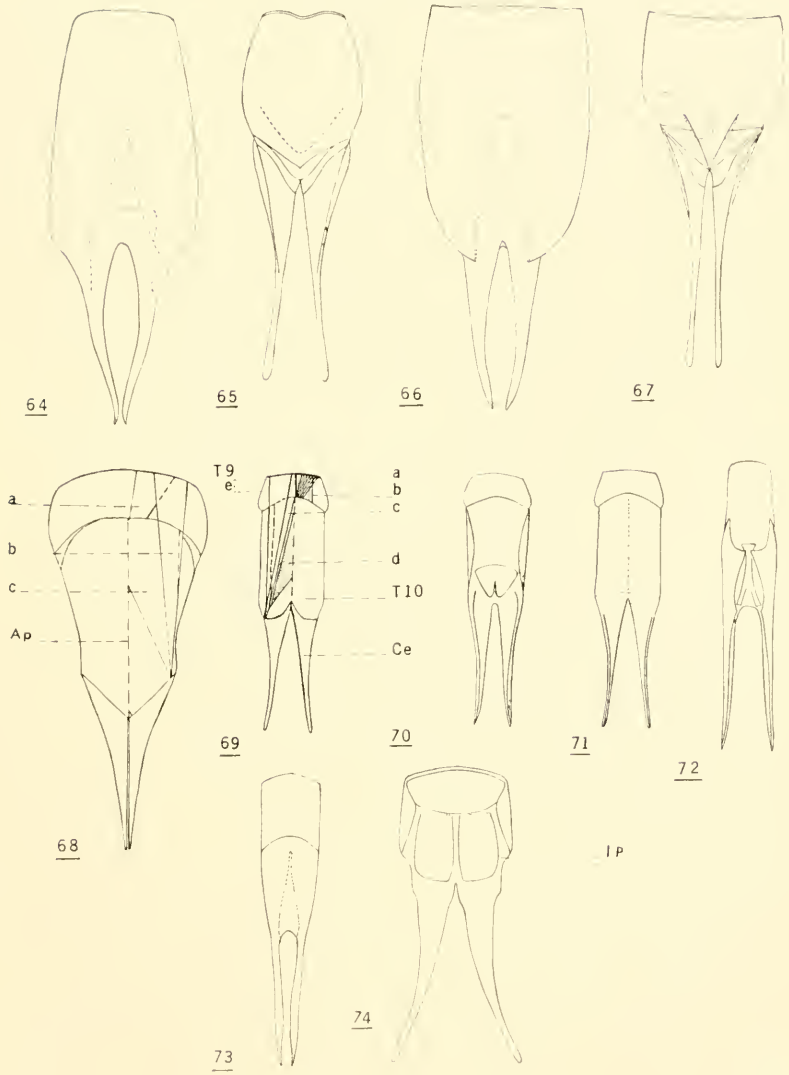


PLATE XIV

FIGS. 75-81.—Accessory glands of females of Tipulinae.

FIG. 75.—*Tipula (Y.) triplex.*

FIG. 76.—*Nephrotoma euceroides.*

FIG. 77.—*Tipula (L.) bicornis.*

FIG. 78.—*Tipula (O.) latipennis.*

FIG. 79.—*Nephrotoma macrocera.*

FIG. 80.—*Tipula (L.) unicincta.*

FIG. 81.—*Tipula (L.) furca.*

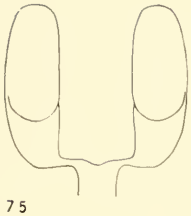
FIG. 82.—Lateral view of terminal abdominal segments of *Tipula (L.) bicornis,* female. Note reduction of cerci to lobes and decrease in size of hypovalves. T10 = tenth tergum; Ce = cercus; H = hypovalve.

FIG. 83.—Ventral view of eighth sternum and hypovalve of *Tipula (L.) bicornis,* female.

FIG. 84.—Ventral view of ninth and tenth terga showing musculature in *Tipula (L.) bicornis,* female. a = muscle from middle of ninth tergum to tenth antecosta; b = muscles from middle of tenth tergum to base of cercus.

FIG. 85.—Dorsal view of terminal abdominal segments of *Tipula (L.) bicornis,* female.

PLATE XIV



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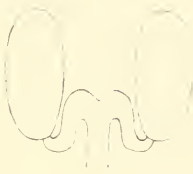

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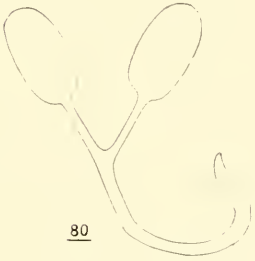

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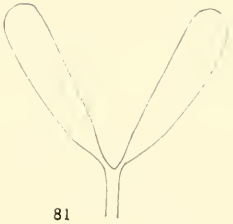

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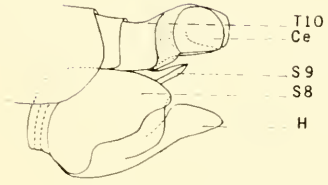

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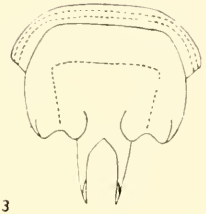

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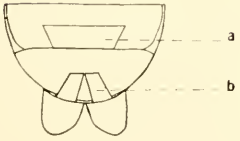

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PLATE XV

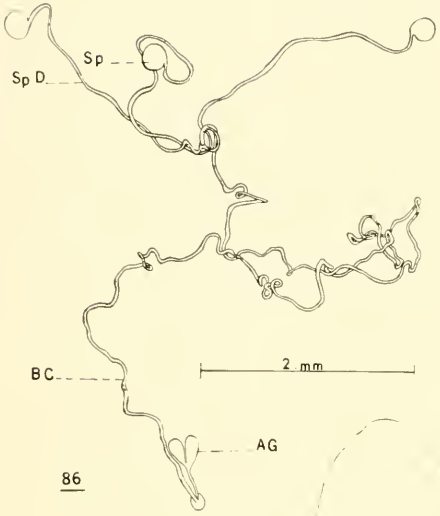
FIG. 86.—Internal reproductive system of *Nephrotoma macrocera*, female. SP = spermatheca; SpD = spermathecal duct; BC = bursa copulatrix; AG = accessory glands. Note that bursa copulatrix is curved at its apex.

FIG. 87.—Dorsal view of vaginal apodeme of *Tipula (Y.) furca*, female.

FIG. 88.—Apical tip of bursa copulatrix in a *Dolichopeza* female. fSp? = possibly the functional spermatheca, as suggested by Byers (1961).

FIG. 89.—Primary genital tract of a *Tipula* female. TF = terminal filament; O = ovary; CO = common oviduct; LAG = lateral "accessory gland" of common oviduct; GO = level of the gonopore.

PLATE XV



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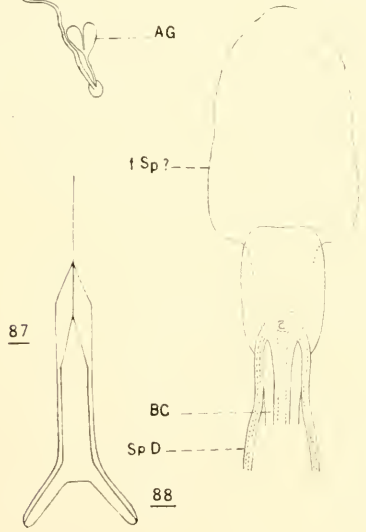

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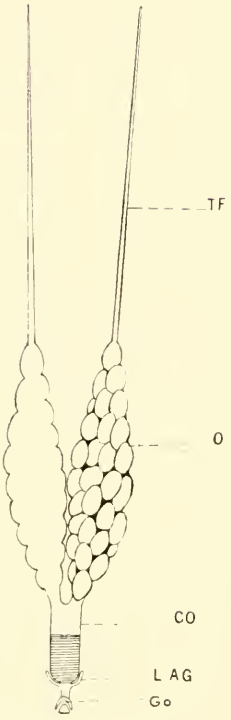

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PLATE XVI

FIG. 90.—Ventral view of ninth sternum and associated parts in *Tipula (L.) triplex,* female. AG = accessory glands; VA = vaginal apodeme; BC = bursa copulatrix; SPD = spermathecal duct; SP = spermatheca.

FIG. 91.—Internal reproductive system of *Tipula (Y.) triplex,* male. Note absence of any swelling in the vas deferens. TS = testes; VD = vas deferens; SV = seminal vesicle; ED = ejaculatory duct; AG = accessory glands.

PLATE XVI

PLATE XVII

FIG. 92.—Caudal view of adminiculum of *Tipula (L.) triplex,* male.

FIG. 93.—Caudal view of adminiculum of *Tipula (Y.) albocaudata,* male.

FIG. 94.—Caudal view of adminiculum of *Tipula (Y.) tricolor,* male.

FIG. 95.—Caudal view of adminiculum of *Tipula (Y.) caloptera,* male.

FIG. 96.—Lateral view of a lateral adminicular arm of *Tipula (Y.) furca,* male.

FIG. 97.—Adminiculum of *Tipula (Y.) furca,* male.

FIG. 98.—Lateral view of adminiculum of *Tipula (Y.) albocaudata,* male.

PLATE XVII

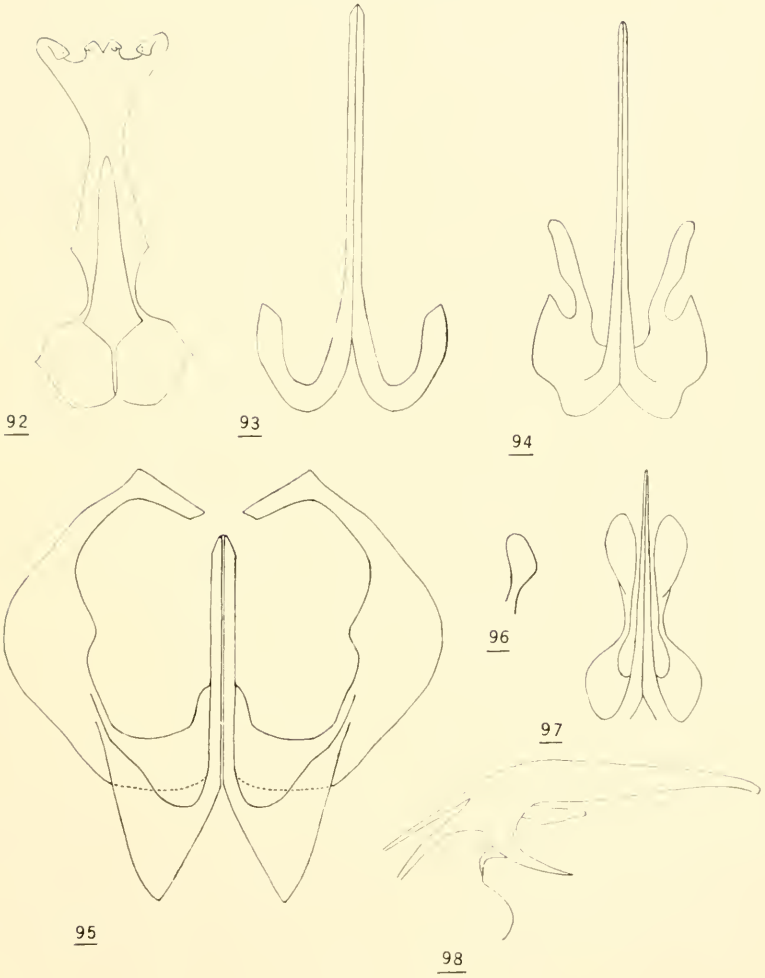


PLATE XVIII

FIG. 99.—Caudal view of adminiculum of *Tipula (L.) bicornis*, male.

FIG. 100.—Vaginal apodeme of *Tipula (Y.) tricolor*, female.

FIG. 101.—Vaginal apodeme of *Tipula (L.) unicincta*, female.

FIG. 102.—Vaginal apodeme of *Tipula (Y.) tephrocephala*, female.

FIG. 103.—Vaginal apodeme of *Tipula (Y.) spernax*, female.

FIG. 104.—Ventral view of eighth abdominal sternum of *Tipula (L.) triplex*, male. Note two sclerotized processes of the sternum, and movable lobes found in the intersegmental membrane of the eighth and ninth segment.

FIG. 105.—Caudal view of the eight abdominal segment of *Tipula (H.) trypetophora*, male.

FIG. 106.—Caudal view of adminiculum (A) and fragmental lobes (F) in *Tipula (L.) dietziana*, male.

FIG. 107.—Caudal view of intersegmental membrane between eighth and ninth sterna in *Tipula (L.) dietziana*, male. Note median sclerite and lateral lobes.

FIG. 108.—Caudal view of adminiculum in *Tipula (L.) australis*, male.

FIG. 109.—Caudal view of adminiculum in *Tipula (T.) oropezoides*, male.

FIG. 110.—Caudal view of base of adminiculum in *Tipula (L.) mohavensis*, male.

FIG. 111.—Sclerite found in dorsal wall of genital chamber in *Tipula (L.) triplex*, male.

FIG. 112.—Shape of sclerotization (only) of anal tubercle in *Tipula (O.) latipennis*, male.

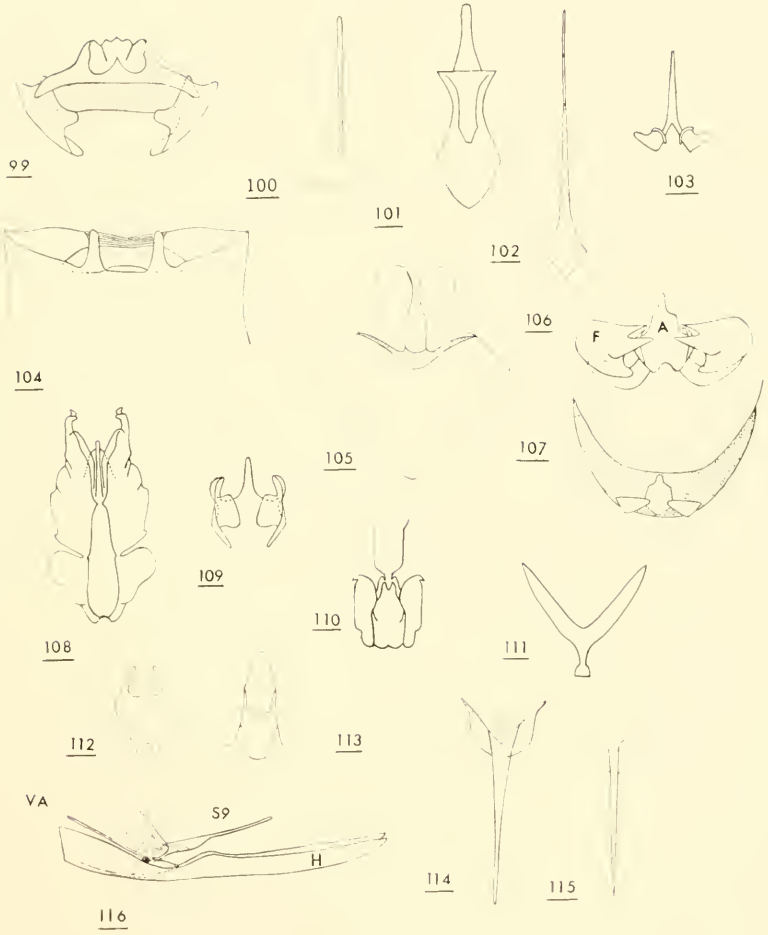
FIG. 113.—Dorsal view of the anal tubercle with its sclerotization in *Tipula (O.) coloradensis*, male.

FIG. 114.—Ninth sternum of *Tipula (L.) triplex*, female.

FIG. 115.—Ninth sternum of *Tipula (Y.) jacobus*, female.

FIG. 116.—Lateral view of terminal abdominal segments of *Ctenophora topazina*, female. Eighth, ninth, and tenth terga including cerci and infra-anal plate do not show. Note blade-like hypovalve (H). The single, undivided dotted line represents the duct of the bursa copulatrix, while the divided one represents the two accessory glands and their common stalk; the dotted lines below represent the common oviduct.

PLATE XVIII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VA
S9
H
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115
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PLATE XIX

FIG. 117.—Dorsal view of ninth sternum of *Tipula (Y.) tricolor,* female.

FIG. 118.—Dorsal view of ninth sternum of *Tripula (Y.) furca,* female.

FIG. 119.—Dorsal view of vaginal apodeme of *Tipula (Y.) caloptera,* female.

FIG. 120.—Dorsal view of ninth sternum of *Tipula (Y.) caloptera,* female.

FIG. 121.—Dorsal view of ninth sternum of *Tipula (Y.) sulfurea,* female.

FIG. 122.—Lateral view of semen pump and intromittent organ of *Holorusia (H.) grandis* male. Note compressor apodeme (CA) between the anterior and posterior immovable apodemes.

PLATE XIX

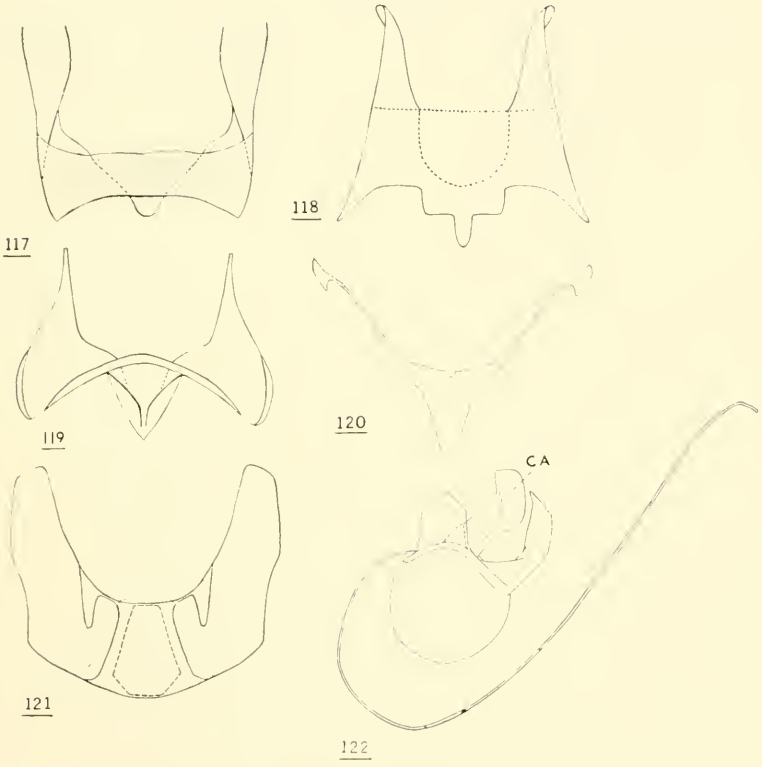
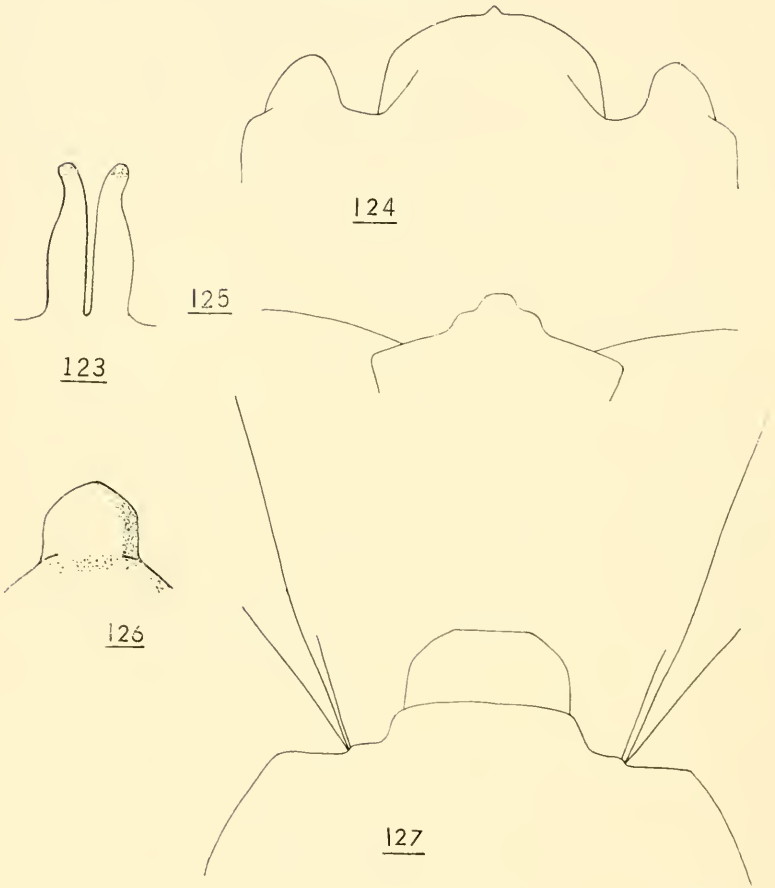


PLATE XX



FIGS. 123-127.—Caudal tip of ninth tergum in males of species of *Tipula*.
FIG. 123.—*Tipula (Y.) albocaudata.*
FIG. 124.—*Tipula (Y.) caloptera.*
FIG. 125.—*Tipula (Y.) spernax.*
FIG. 126.—*Tipula (Y.) furca.*
FIG. 127.—*Tipula (Y.) tricolor.*

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A Revision of the Flies of the Genus *Lespesia* (= *Achaetoneura*) in North America (Diptera: Tachinidae)[1]

BY

DAVID F. BENEWAY

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ABSTRACT: The tachinid fly genus *Lespesia* has been revised for North America. Twenty-one species have been included of which five, *Lespesia callosamiae, L. fasciagaster, L. flavifrons, L. parva,* and *L. sabroskyi,* are described as new. Four specific names have been reduced to synonymy. Separate keys for males and for females have been provided. Thirty-four figures have been included. The well-known generic name *Achaetoneura* has been replaced by the older name, *Lespesia.*

INTRODUCTION

Lespesia is a genus of economically-important parasitic flies, the species of which have been frequently reared from lepidopterous larvae. The genus has not been restudied since the revision by Webber (1930). An attempt to identify specimens by means of his revision frequently reveals that it is inadequate. Many specimens

1. Contribution No. 1161 from the Department of Entomology, University of Kansas, Lawrence, Kansas.

will not key out properly, and determination is often impossible unless the specimen is accompanied by a host record or a puparium. It is therefore the purpose of this revision to provide keys, descriptions and illustrations that will make positive identification feasible in most cases.

Lespesia is an extremely homogeneous genus with respect to visible species characters, and what characters there are cannot always be relied upon. Perhaps the most reliable characters are found in the shapes of the cerci and surstyli of the male terminalia and the shapes of the sclerites of the female postabdomen (see Figs. 7-31). The ratio of the frontal width at vertex to the head width (Figs. 1 and 2) is often useful. Other characters of value include the color of the abdomen, the number of lateral scutellar bristles, the length of the pulvilli of the front tarsi in relation to the last two tarsal segments, the number of antero-dorsal bristles on the middle tibiae, and over-all body size. The host, if known, is also an important clue to identification. The puparia offer some differences among a few species.

It is difficult to state the relationship of *Lespesia* to the rest of the Tachinidae because it falls in the enormous central mass of the family where genera, tribes and subfamilies are exceedingly difficult to define. Perhaps two of the closest genera are *Eufrontina* Brooks and *Frontiniella* Townsend, both of which have three sternopleural bristles as opposed to four in *Lespesia*, differently shaped male terminalia, and a different type of puparium with the stigmal plates protruding to form tubercles. The stigmal plates in the puparium of *Lespesia* are flush with the surface of the puparium. According to Mesnil (personal communication, 1959) *Lespesia* Robineau-Desvoidy, *Descampsia* Mesnil, *Pseudoperichaeta* Brauer and Bergenstamm, *Sturmiopsis* Townsend and *Phryxe* Robineau-Desvoidy constitute a natural group with many morphological and biological characters in common, which may be classified as subfamily Goniinae, tribe Phryxini. Perhaps *Frontiniella* and *Eufrontina* belong in this group but little seems to be known of their biology, so that this is tentative. Some Sturmiini (*e. g.*, the *Sturmia inquinita-distincta* complex) have many morphological characters in common with *Lespesia*. However, these species differ biologically in that they deposit microtype eggs on the food plant of the host, whereas *Lespesia* deposits membranous eggs on the body of the host. Townsend (1941, pt. XI) places *Lespesia* in the family Exoristidae, tribe Phrynoini but Townsend's families and tribes are of doubtful validity due to his extreme tendency towards splitting.

It will not be possible to give a final answer on the relationships of this genus until the central mass of the Tachinidae has been thoroughly studied on a world-wide basis.

MATERIALS AND METHODS

This study was based upon 4,266 specimens, which were distributed as indicated among the following species: *aletiae*, 416; *anisotae*, 156; *archippivora*, 768; *callosamiae*, 55; *ciliata*, 855; *cucullae*, 21; *dimmocki*, 7; *euchaetiae*, 287; *fasciagaster*, 6; *ferruginea*, 2, *frenchii*, 828; *laniiferae*, 2; *melalophae*, 359; *parva*, 2; *pholi*, 26; *rileyi*, 52; *sabroskyi*, 204; *schizurae*, 152; *testacea*, 21; and *texana*, 2.

The specimens were examined under magnifications of ten to forty-five diameters. Drawings were made on squared paper with the aid of an ocular grid. Measurements were taken with an ocular micrometer, at 30 diameters. The head width was measured as seen from the front (Fig. 1). The frontal width at the vertex was measured as seen from above (Fig. 2). The means of these measurements with their standard deviations are given in Tables I and II, p. 677.

Identification is often possible by means of external characters alone, but it is often necessary to examine the male terminalia or the female postabdomen. These structures must be dissected from the specimen to be seen clearly. A number of techniques were tried for dissecting, examining and storing the terminalia of which the following was the most satisfactory. The abdomen was carefully broken off the specimen, placed in a 10% aqueous solution of KOH (caustic potash) and heated to just below the boiling point for about ten minutes or until it was sufficiently relaxed. It was then transferred to slightly acidified 70% alcohol and the terminalia were extracted with fine jeweler's forceps. The abdomen was run through a graded series of alcohols (70%, 95% and 100%) to dry it and was glued back on the specimen. If this is done carefully, the appearance of the specimen is unimpaired. The terminalia were examined by imbedding them in a smear of petroleum jelly on a hanging drop slide and covering them with a few drops of slightly acidified glycerin. The terminalia were stored in microvials which were attached to the pins by running the pin through the cork. Thus the terminalia can be kept with the specimen they come from and there is little chance of their becoming lost. It is important to acidify the glycerin in which the terminalia are stored, otherwise the clearing process will continue and they will disappear.

The terminology employed in this revision is in general that

which is in common usage by students of Diptera. Most of the terms used can be found in Comstock's Introduction to Entomology or Townsend's Manual of Myiology. The terminology of the male and female external reproductive organs has been taken from Crampton (1942). Due to the fusion of the first two abdominal terga in the cyclorrhaphous Diptera, I have begun with tergum two rather than tergum one when counting the abdominal terga from dorsal view.

An attempt has been made to check all synonymies given by Webber by reference to the type specimens. Except where otherwise stated, all species which have been placed in synonymy have been so placed only after reference to the types.

Except where otherwise stated, all locality, host and flight records are based upon specimens that I have examined personally. After each host, the number of flies that have been reared from it is recorded in parentheses. With a few exceptions, the names of Lepidoptera have been taken from McDunnough (1938-39). For the Saturniidae, I have followed Michener (1952).

Throughout this paper reference is occasionally made to code numbers used to label specimens by the Gypsy Moth Laboratory at Melrose Highlands, Massachusetts (*e.g.*, Gip. Moth Lab. 11-776K1). These may be ignored because they represent merely the locality and host of a specimen. Locality and host are given in all such cases and the code numbers are included here only for the sake of completeness.

SYSTEMATIC TREATMENT

Genus *Lespesia* Robineau-Desvoidy

Lespesia Robineau-Desvoidy, 1863, p. 567.

Type: *Erycia ciliata* Macquart, monobasic.

Achaetoneura Brauer and Bergenstamm, 1891, p. 334.

Type: *Achaetoneura hesperus* Brauer and Bergenstamm, designated by Coquillett, 1910, p. 502.

Parafrontina Brauer and Bergenstamm, 1893, p. 115.

Type: *Parafrontina apicalis* Brauer and Bergenstamm.

Rileyella Townsend, 1909, p. 249.

Type: *Tachina aletiae* Riley, by original designation.

Zygofrontina Townsend, 1915, p. 427.

Type: *Zygofrontina capitis* Townsend, by original designation.

Euparafrontina Brèthes, 1917, p. 17.

Type: *Euparafrontina martinezi* Brèthes, monobasic.

Ypophaemyia Townsend, 1916c, p. 75.

Type: *Ypophaemyia malacosomae* Townsend, by original designation.

Masiceropsis Townsend, 1916a, p. 178.

Type: *Masicera pauciseta* Coquillett, by original designation.

Achaetoneuropsis Townsend, 1927, p. 272.

Type: *Achaetoneuropsis affinis* Townsend, by original designation.

I have examined the type specimens of type species of all the above genera except *Erycia ciliata* Macq. and *Euparafrontina martinezi* Brèthes. The latter was synonymized with *Achaetoneura* by Aldrich (1934).

It is with regret and hesitation that I suppress the well-established name *Achaetoneura* in favor of *Lespesia*. However, this change is unavoidable if the law of priority is to be adhered to, as *Lespesia* is the older name. It was adequately described by Robineau-Desvoidy (1863), and the type is well preserved in the Museum National d'Histoire Naturelle, Paris. Mesnil (1950, pp. 105 and 108) was the first to rediscover the name *Lespesia*, and he used that name instead of *Achaetoneura* in Lindner's Die Fliegen der Palaearktischen Region. At my request, Dr. George W. Byers compared specimens of *Achaetoneura* with the type of *Lespesia ciliata* (Macquart), as a result of which there remains little doubt that this type agrees with what has previously been known as *Achaetoneura*.

The use of the name *Achaetoneura* in North America dates to Allen (1926), who pointed out that the type species of *Frontina*, the name previously used for this genus, is *Frontina laeta* Meigen, a European species, which has characters foreign to *Lespesia*, *i. e.*, a different mode of reproduction, strong discal bristles on abdominal terga two and three, the hind tibiae irregularly bristled, the third antennal segment peculiarly slender, etc. *Achaetoneura* was adopted by Allen (1926) and Webber (1930) and has been used up to the present time.

GENERIC DIAGNOSIS

Eyes bare, at most with slight pubescence. Ocellar bristles strong, proclinate. Antennae reaching lowest fourth of face; third segment broad, rounded at apex, never tapering to a point; second segment less than one-third the length of the third; arista bare; second segment of arista about twice as long as wide. Frontal bristles extending below base of third antennal segment. Male with two pairs

of reclinate fronto-orbital bristles which are nearly in line with the bristles of the frontal row, without proclinate fronto-orbitals; female with two pairs of reclinate fronto-orbital bristles as in the male and in addition two pairs of proclinate fronto-orbitals, which lie well outside the frontal row. Ratio of frontal width at vertex to head width always greater in females than in males (see Tables I and II). Parafacials bare; face slightly receding. Facial ridges bristled one-third to two-thirds of the distance from vibrissae to antennal bases. Vibrissae located at level of oral margin; cheeks covered with hair; palpi yellow, well developed; proboscis when fully extended equal in length to about two-thirds of head height.

Thorax gray-pollinose with well developed bristles; mesonotum with four black vittae visible from postero-dorsal view. Chaetotaxy as follows: acrostichals 3:3; dorsocentrals 3:4; intraalars 3:3; intrapostalars 1; supraalars 2:3; humerals 4; notopleurals 2; sternopleurals 4; lateral scutellars 3-4; discal scutellars 1; apical scutellars 1. Apical scutellars usually erect and cruciate. Propleuron bare. Prosternum with weak hairs. Legs black; middle tibiae with one or more strong antero-dorsal bristles near middle; hind tibiae with a row of ciliae on the postero-dorsal surface, with or without a longer bristle near middle. Wings (Fig. 32) hyaline, with normal muscoid venation; cell R_5 open, ending considerably before apex of wing; last section of vein $M_3 + Cu_1$ less than half as long as preceding section; veins bare except base of vein R_{4+5} which has two or three short bristles.

Abdomen without discal bristles on terga 2 to 4; with or without median marginal bristles on terga 2 and 3; if median marginals are present there is never more than one pair on each segment; fourth tergum with a marginal row of bristles; fifth tergum more or less irregularly bristled on entire surface.

Puparium smooth, without spine-like hairs; stigmal plates flat, not protruding to form tubercles; spiracular plates serpentine.

Reproduction by deposition of membranous eggs, ready to hatch, on the body of the host.

KEY TO THE MALES OF THE NORTH AMERICAN SPECIES OF LESPESIA

1. Abdomen black in ground color, predominantly gray-pollinose, without bare red areas except for small red spots laterally on tergum 3. 4
— Abdomen red in ground color, with bare reddish areas covering most of abdomen but always with a black stripe down mid-line of dorsum 2

2. Median marginal bristles absent on abdominal tergum 3 *rileyi*
— Median marginal bristles present on abdominal tergum 3 3
3. Three lateral scutellar bristles *ferruginea*
— Four lateral scutellar bristles *testacea*
4. Three lateral scutellar bristles 5
— Four lateral scutellar bristles 11
5. With a minimum of two strong antero-dorsal bristles near middle of middle tibiae which are equal or subequal in size *dimmocki*
— With only one strong antero-dorsal bristle on middle tibiae; if other bristles are present they are usually only one-half size of strongest bristle 6
6. Pulvilli of front tarsi no longer than last tarsal segment 7
— Pulvilli of front tarsi as long as or longer than last tarsal segment 8
7. Body length 5 mm., abdomen with shining black bands on posterior margins of terga 3 to 5 *parva*
— Body length 5 to 8 mm., abdomen uniformly gray-pollinose without shining black bands on posterior margins of terga 3 to 5 *archippivora*
8. Frontal width at vertex less than .775 mm. *melalophae*
— Frontal width at vertex greater than .775 mm. 9
9. Frontal width at vertex less than .875 mm. *frenchii*
— Frontal width at vertex greater than .875 mm. 10
10. Terminalia with cerci and surstyli long and slender, cerci without a concavity on posterior edge (Fig. 11). (Posterior spiracles of puparium sunken into pits, located on or near the horizontal axis) *ciliata*
— Terminalia with cerci and surstyli short and broad, cerci with a concavity on posterior edge (Fig. 12). [Posterior spiracles of puparium not in pits, located above the horizontal axis (Fig. 34A)] *cuchaetiae*
11. Median marginal bristles present on abdominal terga 2 and 3 16
— Median marginal bristles absent on abdominal terga 2 and/or 3 12
12. Median marginal bristles absent on abdominal terga 2 and 3 *aletiae*
— Median marginal bristles present only on abdominal tergum 3 13
13. Thoracic pollen with a yellowish cast visible to the naked eye; cerci with a concavity on posterior surface (Fig. 15) *pholi*
— Thoracic pollen gray, without a yellowish cast; cerci without a concavity on posterior surface 14
14. Hind tibiae ciliate with a longer bristle near middle; third antennal segment less than 3.0 times length of second *cuculliae*
— Hind tibiae ciliate, usually without a longer bristle; third antennal segment more than 3.0 times length of second 15
15. Abdomen with a yellowish cast; Mexico *laniiferae*
— Abdomen without a yellowish cast; North America *schizurae*
16. Abdomen gray-pollinose, marked by bare shining black bands on posterior margins of terga 3 to 5 *fasciagaster*
— Abdomen uniformly gray-pollinose, without bare shining black bands on posterior margins of terga 3 to 5 17
17. Face and front bright yellow-pollinose 18
— Face and front gray-pollinose, at most only slightly tinged with yellow 19

18. Facial depression yellow-pollinose ... *texana*
— Facial depression gray-pollinose ... *flavifrons*
19. Wings with distance from crossvein r-m to tip of vein R_{4+5} 3.39 mm. or more; body length usually 10 mm. or more ... 20
— Wings with distance from crossvein r-m to tip of vein R_{4+5} 3.24 mm. or less; body length usually 9 mm. or less ... 22
20. Cerci and surstyli long, slender and attenuated (Fig. 8) ... *datanarum*
— Cerci and surstyli broad (Figs. 10 and 18) ... 21
21. Surstyli with a distinct convexity on their posterior edge (Fig. 10) ... *callosamiae*
— Surstyli without a distinct convexity on their posterior edge (Fig. 18). ... *sabroskyi*
22. Frontal width at vertex less than .875 mm. ... *frenchii*
— Frontal width at vertex greater than .875 mm. ... 23
23. Eyes with distinct pubescence visible at high magnification; two to three strong antero-dorsal bristles on middle tibiae ... *dimmocki*
— Eyes at most with only slight pubescence visible at high magnification; one strong antero-dorsal bristle on middle tibiae ... 24
24. Terminalia with cerci and surstyli long and slender, cerci without a concavity on posterior edge (Fig. 11). (Posterior spiracles of puparium sunken into pits, located on or near the horizontal axis.). ... *ciliata*
— Terminalia with cerci and surstyli short and broad; cerci with a concavity on posterior edge (Fig. 12). [Posterior spiracles of puparium not in pits, located above the horizontal axis (Fig. 34A).]. ... *cuchaetiae*

KEY TO THE FEMALES OF THE NORTH AMERICAN SPECIES OF *Lespesia*

1. Abdomen black in ground color, predominantly gray-pollinose, without bare red areas except for small red spots laterally on tergum 3. ... 4
— Abdomen red in ground color, with bare reddish areas covering most of abdomen but always with a black stripe down mid-line of dorsum ... 2
2. Median marginal bristles absent on abdominal tergum 3; hind tibiae ciliate, usually without a longer bristle near middle ... *rileyi*
— Median marginal bristles present on abdominal tergum 3; hind tibiae ciliate with a longer bristle near middle ... 3
3. Three lateral scutellar bristles ... *ferruginea*
— Four lateral scutellar bristles ... *testacea*
4. Three lateral scutellar bristles ... 5
— Four lateral scutellar bristles ... 11
5. With a minimum of two strong antero-dorsal bristles near middle of middle tibiae which are equal or subequal in size ... *dimmocki*
— With only one strong antero-dorsal bristle on middle tibiae; if other bristles are present they are at most one-half the size of the strongest bristle ... 6

6. Abdomen with bare and shining black bands on posterior margins of terga 3 to 5; body length 5 mm. *parva*
— Abdomen uniformly gray-pollinose without shining black bands on posterior margins of terga 3 to 5; body length usually greater than 5 mm. 7
7. Frontal width at vertex less than .85 mm.; face and front with a pronounced yellowish cast *melalophae*
— Frontal width at vertex greater than .85 mm.; face and front with at most a slight yellowish cast 8
8. Ratio of frontal width at vertex to head width .408 ± .0112. *archippivora*
— Ratio of front width at vertex to head width .380 ± .0137 or less. 9
9. Ratio of frontal width at vertex to head width .366 ± .0124; host usually *Euchaetias egle* *euchaetiae*
— Ratio of frontal width at vertex to head width greater than above; host not *Euchaetias egle* 10
10. Ratio of frontal width at vertex to head width .376 ± .0149; posterior spiracles of puparium sunken into pits; host *Hyalophora* spp. *ciliata*
— Ratio of frontal width at vertex to head width .380 ± .0137; posterior spiracles of puparium flush with surface of puparium; host not *Hyalophora* spp. *frenchii*
11. Median marginal bristles present on abdominal terga 2 and 3 16
— Median marginal bristles absent on abdominal terga 2 and/or 3 12
12. Median marginal bristles absent on abdominal terga 2 and 3 *aletiae*
— Median marginal bristles present only on abdominal tergum 3 13
13. Thoracic pollen with a yellowish cast visible to the naked eye *pholi*
— Thoracic pollen gray, at most with only a slight yellowish cast 14
14. Hind tibiae ciliate with a longer bristle near middle; third antennal segment less than 3.0 times length of second *cuculliae*
— Hind tibiae ciliate, usually without a longer bristle; third antennal segment more than 3.0 times length of second 15
15. Abdomen with a yellowish cast; Mexico *laniiferae*
— Abdomen without a yellowish cast; North America *schizurae*
16. Abdomen gray-pollinose, marked by bare shining black bands on posterior margins of terga 3 to 5 *fasciagaster*
— Abdomen uniformly gray-pollinose, without bare shining black bands on posterior margins of terga 3 to 5 17
17. Face and front bright yellow-pollinose 18
— Face and front gray-pollinose, at most only slightly tinged with yellow 19
18. Facial depression yellow-pollinose *texana*
— Facial depression gray-pollinose *flavifrons*
19. Wings with distance from crossvein r-m to tip of vein R_{4+5} 3.39 ± .436 mm.; body length usually 10 mm. or more 20
— Wings with distance from crossvein r-m to tip of vein R_{4+5} 3.19 ± .182 mm. or less; body length usually 9 mm. or less 22
20. Postabdomen as in Fig. 20 *datanarum*
— Postabdomen as in Figs. 22 and 27 21

21. Postabdomen as in Fig. 22; host *Hyalophora promethea* . . . *callosamiae*
— Postabdomen as in Fig. 27; hosts *Antheraea polyphemus* and *Automeris io* . . . *sabroskyi*
22. Eyes with distinct pubescence visible under high magnification; two to three strong antero-dorsal bristles on middle tibiae; abdomen with a longitudinal band of erect hairs extending along mid-line of dorsum which are in sharp contrast to the adjacent depressed hairs . . . *dimmocki*
— Eyes with at most slight pubescence visible under high magnification; one strong antero-dorsal bristle on middle tibiae; abdominal hairs uniformly depressed . . . 23
23. Ratio of frontal width at vertex to head width .366 ± .0124; host usually *Euchaetias egle* . . . *euchaetiae*
— Ratio of frontal width at vertex to head width greater than above; host not *Euchaetias egle* . . . 24
24. Ratio of frontal width at vertex to head width .376 ± .0149; (posterior spiracles of puparium sunken into pits); host *Hyalophora* spp. . . . *ciliata*
— Ratio of frontal width at vertex to head width .380 ± .0137; (posterior spiracles of puparium flush with surface of puparium); host not *Hyalophora* spp. . . . *frenchii*

DESCRIPTIONS

Lespesia aletiae (Riley), new combination

FIGURES 7, 19, 28

Tachina aletiae Riley, 1879, p. 162.
Tachina fraterna Comstock, 1879, p. 303.
Achaetoneura aletiae, Allen, 1926, p. 188; Webber, 1930, p. 26; Patton, 1958, p. 31.

A medium-sized species, over-all length about 8 mm. Distinguished from *rileyi* by having a dense, gray-pollinosity on the abdomen, whereas the abdomen in *rileyi* has extensive, bare, reddish areas. Distinguished from all other species of the genus by the absence of median marginal bristles on abdominal terga 2 and 3.

Male: Eyes with slight pubescence visible at high magnification. Face, front, and occipital orbits gray-pollinose, with a yellowish cast. Second and third antennal segments black. Arista tapered nearly uniformly for its entire length, thickened slightly on basal half. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong; outer verticals weak, scarcely differentiated from hairs of occipital fringe. Parafrontals with scattered black hairs outside frontal row, none of which is equal in size to the bristles of frontal row. Facial ridges bristled for about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about

one-third width of front. Bristles of occipital fringe in a double row, but posterior row irregular and weak. Beard thick, composed of white hairs.

Thorax gray-pollinose, sometimes with a yellowish cast. Mesonotum with four poorly defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black and shining except for posterior surface of front femur, which is lightly gray-pollinose. Pulvilli of front tarsi about equal in length to last tarsal segment. Middle tibiae with one strong antero-dorsal bristle but no other bristles developed. Hind tibiae evenly ciliate, with one longer bristle near middle.

Abdomen black in ground color, gray-pollinose, without a yellowish cast, sometimes with a reddish spot laterally, extending from terga 2 to 4, but with the reddish area never so extensive as in *rileyi*, *testacea*, and *ferruginea*. Median marginal bristles lacking on abdominal terga 2 and 3; fourth tergum with a marginal row of bristles; fifth tergum with an irregular row of bristles near apex. Terminalia (Fig. 7) distinctive; surstyli short and broad, cerci about the same length as surstyli but not so broad in relation to their length.

Female: Outer vertical bristles weak, about one-fourth size of inner verticals; pulvilli of front tarsi shorter than last tarsal segment; abdomen almost entirely covered with gray pollen which has a slight yellowish cast on tergum 5; if reddish areas are present they are usually small; tergum 5 of abdomen without a well-defined row of bristles near apex but covered with large erect hairs on entire surface. Postabdomen (Figs. 19 and 28) distinctive, long and attenuated.

Measurements: See Tables I and II.

Types: Riley's type appears to be lost and cannot be located in the U. S. National Museum. Webber (1930) redescribed the species from one male and two females from Centerville, Florida, Nov. 23, 1878, reared from *Alabama argillacea* Hübner (= *xylina* Say). The specimens are labeled "468L08, par. on *A. xylina*, iss. Nov. 23, 1878." Webber did not designate a neotype. I have examined the aforementioned specimens and have used them as a basis for subsequent identifications. Since *aletiae* is a distinctive and easily recognized species, there seems little doubt that it has been correctly identified.

Hosts: Amatidae: *Syntomeida epilais* (11). Arctiidae: *Dia-*

crisia virginica (3), *Estigmene acrea* (4), *Estigmene* sp. (1), *Halisidota harrisii* (60), *Halisidota* sp. (1), *Hyphantria cunea* (7), *Hyphantria* sp. (1), *Seirarctia echo* (1), and *Utetheisa bella* (2). Hesperiidae: *Epargyreus tityrus* (2) and *Urbanus proteus* (1). Lasiocampidae: *Malacosoma americana* (2). Lymantriidae: *Hemerocampa leucostigma* (26) and *Orygia* sp. (1). Megalopygidae: *Megalopyge opercularis* (4) and *Megalopyge* sp. (1). Noctuidae: *Alabama argillacea* (1), *Heliothis* sp. (2), *Laphygma frugiperda* (1), *Pseudaletia unipuncta* (2), *Trichoplusia ni* (1), and *Xanthopastis timais* (2). Notodontidae: *Datana ministra* (3). Nymphalidae: *Apatura* sp. (8), *Nymphalis antiopa* (3), *Polygonia interrogationis* (1), and *Vanessa cardui* (1). Pieridae: *Pieris protodice* (3) and *P. rapae* (23). Pyralidae: *Evergestis rimosalis* (1). Sphingidae: *Ceratomia catalpae* (3). In addition to the above records from Lepidoptera, I have one record from *Epilachna corrupta* (Coleoptera: Coccinellidae).

Distribution: Ontario southward to southern Florida, westward to Arizona. *Ontario:* Port Erie. *Alabama:* Birmingham. *Arizona:* Ruby. *Arkansas:* Fayetteville. *California:* Los Angeles Co. and Watts. *District of Columbia:* Washington. *Florida:* Alford; Biscayne Bay; Centerville; Daytona; Gainesville; Homestead, Dade Co.; Larkins, Levy Co.; Ocala and St. Petersburg. *Georgia:* Savannah. *Illinois:* Carlinville and Sanbury. *Indiana:* Lafayette. *Louisiana:* Baton Rouge and Mt. Heyman. *Maryland:* Hagerstown. *Mississippi:* Agricultural and Mechanical College; Gulfport and Pascagoula. *Missouri:* Benton; Charleston and Sikeston. *New Jersey:* Burlington; Readington; Somerville; Trenton and West Long Branch. *New Mexico:* Albuquerque. *New York:* Brooklyn. *North Carolina:* Willard. *Oklahoma:* Durant. *Pennsylvania:* Philadelphia. *South Carolina:* Florence. *Tennessee:* Hurricane Mills; Monroe Co. and Nashville. *Texas:* College Station; Comfort; Shamrock and Victoria. *Virginia:* Accomac Co.; Arlington; Diamond Springs; Falls Church; Norfolk; Northampton Co.; Ravensworth; Rosslyn and Vienna.

Flight records: North of the 38th parallel, this species appears to have two peaks of abundance, one in July and another in September and October. Therefore, there may be two broods. South of the 38th parallel the flight records extend later into the fall and winter and begin earlier in the spring.

Lespesia archippivora (Riley), new combination

Figures 4, 5, 6, 9, 21

Tachina archippivora Riley, 1871, p. 150.
Masicera archippivora, Williston, 1889, p. 1923.
Meigenia websteri Townsend, 1891c, p. 206.
Phorocera promiscua Townsend, 1891a, p. 84.
Ypophaemyia malacosomae Townsend, 1916c, p. 75.
Parafrontina apicalis Braner and Bergenstamm, 1893, p. 115.
Masicera paucisceta Coquillett, 1897, p. 114.
Masiceropsis paucisceta, Townsend, 1916a, p. 178.
Achaetoneura archippivora, Allen, 1926, p. 196; Webber, 1930, p. 20; Patton, 1958, p. 32; Butler, 1958, p. 561.

Webber (1930, p. 20) erroneously credited the name *archippivora* to Williston (1889) rather than Riley (1871). However, Riley did propose the name and did give a crude description. Therefore, the name is here credited to Riley.

A small species, over-all length 5 to 7 mm. The males are distinguished from all other species except *parva* by the pulvilli of the front tarsi which are shorter than the last tarsal segments, and from *parva* by their larger size. The females can be separated from *parva* by their larger size; from *fasciagaster* by the lack of black bands on the abdominal tergites; and from all other species by a ratio of frontal width at vertex to head width of .408 ± .0112 (all other species have a smaller ratio than this).

Male: Head (Fig. 4) with eyes having slight pubescence visible at high magnification. Face and front gray-pollinose, former with a faint yellowish cast. Antennae mostly black, third antennal segment reddish only at extreme base, second segment with a reddish cast. Arista thickened on basal half, tapered rapidly apically. Frontal bristles about nine in number, extending to just below base of third antennal segment. Inner vertical bristles strong; outer verticals well developed, about one-half size of inner verticals. Parafrontals with scattered black hairs outside frontal row, none of which is equal in size to bristles of frontal row. Facial ridges bristled about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-fourth width of front. Bristles of occipital fringe in a double row but posterior row irregular and weak. Beard thick, composed of white hairs.

Thorax gray-pollinose. Mesonotum with four rather well defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black and shining, with a

reddish tinge, except for posterior surface of front femur, which is thinly gray-pollinose. Pulvilli of front tarsi shorter than last tarsal segment. Middle tibiae with one strong antero-dorsal bristle, no other bristles developed. Hind tibiae ciliate with one longer bristle near middle.

Abdomen black in ground color, gray-pollinose without a yellowish cast with exception of fifth tergum; occasionally a bare red spot present laterally on tergum 3. Median marginal bristles present or absent on tergum 2; present on tergum 3; third tergum with a marginal row of bristles; fifth tergum irregularly bristled on apical half. Terminalia (Fig. 9) similar to those of *melalophae*.

Female: Second antennal segment more reddish. Otherwise similar to male.

Measurements: See Tables I and II.

Types: Redescribed from three female syntypes (No. 2840, U. S. N. M.) and one male from the same locality as the types, without further data except a label bearing the number *60*. These specimens are in the U. S. National Museum. They are apparently the specimens Riley had before him when he described the species because the *60* seems to correspond to code numbers found in some old notes made by Riley at the time he reared the flies. It would be very difficult to prove otherwise at this late date; hence these specimens are here accepted as the types. They were reared from *Danaus plexippus* (L.) at St. Louis, Missouri.

Hosts: Arctiidae: *Estigmene acrea* (9) and *Estigmene* sp. (1). Danaidae: *Danaus berenice* (3) and *D. plexippus* (150). Lasiocampidae: *Malacosoma americana* (31), *M. constricta* (1), *M. disstria* (1), *M. pluvialis* (2), and *Malacosoma* sp. (4). Noctuidae: *Agrotis ypsilon* (1), *Euxoa vestigialis* (1), *Feltia subterranea* (1), *Laphygma exigua* (2), *Prodenia praefica* (1), *Prodenia* sp. (2), and *Scotogramma trifolii* (1). Notodontidae: *Schizura concinna* (1). Nymphalidae: *Nymphalis antiopa* (4), *Vanessa atalanta* (20), *V. cardui* (15), and *V. caryae* (7). Papilionidae: *Papilio* sp. (1). Pyralidae: *Loxostege sticticalis* (19). Pieridae: *Pieris protodice* (12), *P. rapae* (17), and *Pieris* sp. (2). In addition to these records from Lepidoptera, I have one record from *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae).

Distribution: British Columbia to Ontario, southward to Florida and southern Mexico and westward to California, Oregon and Washington. *Alberta:* Lethbridge. *British Columbia:* Kamloops. *Ontario:* Toronto and Wade. *Mexico:* Atzcapotzalco; Elta Clax;

Hermosilla; Los Mochis; Mexico D. F. and Tepexpan. *Arizona:* Buckeye; 20 mi. N. Flagstaff; Hot Springs; Phoenix; Sahuarita; Seligman; south fork Cave Creek Canyon, Chiricahua Mountains; Tempe; Thatcher; Topock and Yuma. *Arkansas:* Sebastian Co. and Washington Co. *California:* Alameda Co.; Alum Rock Park, Santa Clara Co.; Antioch, Contra Costa Co.; Amboy, San Bernardino Co.; Apple Valley, San Bernardino Co.; Berkeley; Brawley; Carlsbad; Cherry Valley; Chula Vista; Claremont; Compton; Davis; El Centro; Firebaugh, Fresno Co.; Gilroy; Hopkins Well, Riverside Co.; 6 mi. W. Indio, Riverside Co.; Isleton; 25 mi. S. Ivanpah, San Bernardino Co.; Kramer Hills, San Bernardino Co.; Lindsay; Los Alamitos; Los Angeles Co.; Macy; Mono Lake; Mt. Diablo, Contra Costa Co.; Niland, Imperial Co.; Palo Alto; Patterson, Stanislaus Co.; Pleasanton; Riverside; Redwood City, Tulare Co.; Sacramento; San Joaquin; San Jose; San Mateo; Saticoy; Saugus; Seal Beach; Shafter; Spreckels; Tracy, San Joachin Co.; Westmoreland; Whittier and Wood Lake, Tulare Co. *Florida:* Belle Glade. *Georgia:* Griffin. *Idaho:* Jerome; Lewiston and Moscow. *Illinois:* Cambridge; Carbondale; Carlinville and Urbana. *Indiana:* Attica and Lafayette. *Iowa:* Ames and Mount Ayr. *Kansas:* Garden City; Lawrence; Leavenworth Co. and Wellington. *Louisiana:* Baton Rouge. *Maine:* Augusta; Ellsworth; Glenburn and Ogunquit. *Maryland:* Hagerstown. *Massachusetts:* Amherst; Cambridge; Chicopee; Lexington; Melrose Highlands; Revere; near Salem and Wakefield *Michigan:* Cheboygan Co. and Emmett Co. *Mississippi:* Agricultural and Mechanical College; Hamburg and Tupelo. *Missouri:* Atherton and St. Louis. *Nebraska:* North Platte. *Nevada:* Baker. *New Hampshire:* Claremont. *New Jersey:* North Branch and Somerville. *New Mexico:* Beulah; Koehler; Malaya; Mesilla and Roswell. *New York:* Albany; Hebron; Ithaca; Lake Placid and Slingerlands. *Ohio:* Lima; Miami Co. and Sandusky. *Oregon:* Klamath Falls and Vale. *Pennsylvania:* Lancaster and New Wilmington. *South Carolina:* St. Matthews. *South Dakota:* Brookings. *Tennessee:* Clarksville; Hurricane Mills and Nashville. *Texas:* Bexar Co.; Brownsville; Chillicothe; College Station; Dallas; Raymondsville; San Diego; Sinton; Spur and Victoria. *Utah:* Birch Glen; Delta; Elberta; Granite; Lewiston; Logan; Midvale; Mono; Monticello; Nibley; Provo; Richardson; Roy; Rush Lake, Iron Co.; Smithfield and Vernal. *Virginia:* Norfolk. *Washington:* Edwall; Lind and Pullman. *Wisconsin:* Madison.

Flight records: North of the 38th parallel, this species is most

common from July through September. For both June and October, I have approximately one-third as many records as for any one of the peak months of July through September. South of the 38th parallel, scattered records extend throughout the winter.

Lespesia callosamiae, n. sp.

FIGURES 10, 22

A large-sized species, over-all length 10 to 12 mm. Extremely close to *sabroskyi*, from which it can be separated by the form of the male terminalia (Figs. 10 and 18) and the female postabdomen (Figs. 22 and 27), and by the host, if known. *L. callosamiae* has been reared only from *Hyalophora promethea* whereas *L. sabroskyi* has been reared from *Antheraea polyphemus, Automeris io* and *H. curyalus*. This species is similar in size to *datanarum* from which it may be separated by the shape of the male terminalia (Figs. 10 and 8) and the female postabdomen (Figs. 22 and 20). Other species which are morphologically similar to *callosamiae* such as *euchaetiae, ciliata,* and *frenchii* may usually be separated from *callosamiae* by their smaller body size.

Male: Eyes with very slight pubescence visible at high magnification. Face and front gray-pollinose, both with a yellowish cast. Second and third antennal segments black. Arista thickened on basal one-half, tapered rapidly apically. Frontal bristles about ten in number, extending to below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-third size of inner verticals. Parafrontals with scattered black hairs outside frontal row and a row of hairs parallel to frontal row, all of which are much smaller than bristles of frontal row. Facial ridges bristled for about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row fairly regular. Beard of medium thickness, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four poorly defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black and shining, with a reddish tinge, with very little pollen except for posterior surface of front femur, which is gray-pollinose. Pulvilli of front tarsi about as long as last tarsal segment. Middle tibiae with

one strong antero-dorsal bristle near middle and usually another bristle about one-third the size of strong bristle. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color, gray-pollinose with a slight yellowish cast which is most pronounced on tergum 5. Tergum 3 usually with a red spot laterally which may extend to terga 2 and 4. Terga 2 and 3 each with one pair of median marginal bristles; tergum 4 with a marginal row of bristles; tergum 5 with an irregular row of bristles at about two-thirds distance from base to apex. Terminalia (Fig. 10) distinctive, sursyli with a distinct convexity on their posterior edge.

Female: Pulvilli of front tarsi shorter than last tarsal segment; postabdomen (Fig. 22) similar to that of *euchaetiae.* Otherwise similar to male.

Measurements: See Tables I and II.

Types: Described from 25 specimens, all of which were reared from *Hylaphora promethea.* Holotype, male, Milford, Connecticut, July 8, 1918, Gip. Moth Lab. 12128P4. Allotype, female, Rutherford, New Jersey, July 3, 1916, Gip. Moth Lab. 10059. Paratypes, 15 males and 8 females from the following localities. *Connecticut:* Milford, July 10, 1928, Gip. Moth Lab. 12128P4; New Haven, June 29-July 2, 1928, Gip. Moth Lab. 12128P7. *New Jersey:* Rutherford, June 5-July 24, 1916, July 16, 1917, Gip. Moth Lab. 10059. *New York:* Coonrad, July 23, 1938, Gip. Moth Lab. 12128N6; Rochester, July 25, 1916, Gip. Moth Lab. 10060A. *Ohio:* Bratenahl, July 28, 1916, Gip. Moth Lab. 10059F. The entire type series is in the U. S. National Museum.

Host: Saturniidae: *Hylaphora promethea* (42).

Distribution: In addition to the locality records taken from the type series, the following locality records are represented by 30 specimens not included in the type series. *Ontario:* Marmora and Roseland. *Maryland:* Prince George Co. *New Jersey:* Orange; Parlin; Rathway and Trenton. *New York:* Chemung and East Aurora. *Oregon:* Eugene and vicinity. *Pennsylvania:* Berwyn; Harrisburg; Indiana; Ingrain and Shamokin. *Virginia:* Falls Church.

Flight records: This species has been most frequently collected during July.

Lespesia ciliata (Macquart)

FIGURES 11, 23, 30

Erycia ciliata Macquart, 1834, p. 294.
Lespesia ciliata, Robineau-Desvoidy, 1863, p. 569.
Achaetoneura samiae Webber, 1930, p. 15 (new synonymy).

Robineau-Desvoidy (1863, p. 569) based *Lespesia ciliata* on a specimen in the Museum National d'Histoire Naturelle, Paris labeled *Masicera ciliata* Macquart for which he never found a published description. Mr. Curtis Sabrosky (personal communication, 1960) believes that this species was originally published as *Erycia ciliata* as cited above.

I have not examined the type of *Lespesia ciliata* but Dr. George W. Byers kindly examined it at my request. He compared several species of *Lespesia* with this type and found that what has been known as *samiae* agreed with it.

Since *ciliata* was the sole species included in *Lespesia* by Robineau-Desvoidy, it becomes type species of the genus by monotypy.

Since *Lespesia* as circumscribed here is exclusively Nearctic, there remains some doubt as to how Robineau-Desvoidy happened to include it in a treatise on the Diptera of the Paris area. Mesnil (1950) speculates that some saturnid larvae may have been shipped to France from the United States in the hope that they would produce silk well enough to take the place of the silkworm, *Bombyx mori*, which had been decimated by a disease. The specimen in question may have been reared from such a saturnid larva, and subsequently placed in the collection of Macquart in the Paris museum.

A medium-sized species, over-all length 7 to 9 mm. It is most readily recognized by its puparium, which has the posterior spiracles located in a depression on the horizontal axis. All other species have the posterior spiracles of the puparium flush with the surface of the puparium.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, both with a yellowish cast. Second antennal segment black with a reddish tinge, third antennal segment black. Arista thickened on basal two-thirds, tapered rapidly apically. Frontal bristles about ten in number, extending to below base of third antennal segment. Inner vertical bristles strong, outer vertical bristles about one-fourth size of inner verticals. Parafrontals with a row of hairs outside frontal row which may be as large as one-half size of the bristles of frontal row. Facial ridges bristled about two-thirds distance from vibrissae to antennal bases, bristles

in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row very irregular. Beard of moderate thickness, composed of white hairs.

Thorax black in ground color, gray-pollinose without a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three or four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a faint reddish tinge, without pollen except for posterior surface of front femur. Pulvilli of front tarsi a little longer than last tarsal segment. Middle tibiae with one strong antero-dorsal bristle near middle and usually another bristle about one-half size of strongest bristle. Hind tibiae evenly ciliate, with one longer bristle near middle.

Abdomen black in ground color, heavily gray-pollinose, without a yellowish cast except for fifth tergum. Tergum 3 usually with bare red spots laterally. Median marginal bristles present on abdominal terga 2 and 3; fourth tergum with a marginal row; fifth tergum more or less bristled on entire surface. Terminalia (Fig. 11) similar to those of *datanarum;* cerci and surstyli long and attenuated.

Female: Outer vertical bristles stronger, about one-half size of inner verticals; third antennal segment more reddish, reddish on at least basal half; pulvilli of front tarsi shorter than last tarsal segment; postabdomen (Figs. 23, 30) distinctive, short and broad.

Measurements: See Tables I and II.

Type: Holotype, male, labelled "Salia eclose d'un Bombyx" (no other data), in the Museum National d'Histoire Naturelle, Paris, France. The type locality remains in doubt because it is not known where the caterpillar from which the fly emerged originated.

Hosts: Saturniidae: *Hyalophora cecropia* (353), *H. columbia nokomis* (23), *H. gloveri* (12), *H. euryalus* (15), and *Hyalophora* sp. (18).

Distribution: From British Columbia eastward to Nova Scotia, southward to the District of Columbia and westward to California and Oregon. *British Columbia:* Fernie and Kaslo. *Manitoba:* Aweme; Cartwright and Transcoma. *New Brunswick:* Fredricton and Sunbury. *Nova Scotia:* Hunts Co.; Kings Co. and Truro. *Ontario:* L'Orignal; Ottawa and Steenburg. *Quebec:* Montreal. *Saskatchewan:* Saskatoon. *Arizona:* Palmerlee. *California:* San Bernardino Mts.; and West Pittsburg, Contra Costa Co. *Connecticut:*

Ellington and Mansfield. *District of Columbia:* Washington. *Maine:* Bangor; Bar Harbor; Carmel; Fryeburg; Norway; Orono and Waterville. *Massachusetts:* Amherst; Boxford and North Saugus. *New Hampshire:* Durham and Greenfield. *New Jersey:* Berlin; Green Village; Lakehurst and Rutherford. *New York:* Albany; Fisher's Island; Ithaca; Kingston; Margaretville; Putnam and Putnam Valley. *Oregon:* Corvallis. *Rhode Island:* Newport. *Utah:* Stockton.

Flight records: This is apparently an early season species. North of the 38th parallel, most of the records are for April and May. However, a good many of these records are for reared specimens which emerged from pupae which had been kept indoors over the winter. Therefore, the majority of the flies probably emerged earlier than they would have in nature.

Lespesia cuculliae (Webber), new combination

FIGURE 24

Achaetoneura cuculliae Webber, 1930, p. 18; Patton, 1958, p. 32.

A medium-sized species, length 8 to 10 mm. It is separated from all other species except *pholi, laniiferae,* and *schizurae* by median marginal bristles which are absent on abdominal tergum 2 but present on abdominal tergum 3. It can be separated from *pholi* by the lack of a yellowish cast in the thoracic pollen; from *laniiferae* by the presence of a longer bristle in the ciliate row on the hind tibiae; and from *schizurae* by the third antennal segment which is less than 3.0 times the length of the second.

Female: Eyes with very slight pubescence visible at high magnification. Face, front and posterior surface of head silvery gray-pollinose, usually without a yellowish cast although an occasional specimen is encountered which is distinctly golden-pollinose in these regions. Second and third antennal segments black; third antennal segment less than 3.0 times length of the second (in all other species the third antennal segment is more than 3.0 times length of second). Arista thickened on basal one-half, tapered rapidly apically. Frontal bristles about eight in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-third size of inner verticals. Parafrontals with very small scattered black hairs outside the frontal row none of which is equal in size to the bristles of frontal row. Facial ridges bristled weakly about one-third distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta

brown, about one-fourth width of front. Bristles of occipital fringe in a double row, posterior row fairly strong and regular. Beard of medium thickness, composed of white hairs.

Thorax gray-pollinose and usually without a yellowish cast. Mesonotum with four well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles cruciate, sometimes erect and sometimes recumbent. Legs black with a reddish tinge, bare and shining, except for posterior surface of front femur, which is lightly gray-pollinose. Pulvilli of front tarsi shorter than last tarsal segment. Middle tibiae with one strong antero-dorsal bristle near middle; if other bristles are developed they are very weak. Hind tibiae ciliate with one longer bristle near middle.

Abdomen black in ground color, heavily gray-pollinose; fifth tergum with a slight yellowish cast; usually without a bare red spot laterally. Median marginal bristles absent on tergum 2; present on tergum 3; fourth tergum with a strong marginal row; fifth tergum heavily covered with large scattered bristles on apical half which are not in rows. Postabdomen (Fig. 24) distinctive, short and broad.

Male: Unknown. Webber (1930, p. 19) described the species from one female but placed specimens of both sexes together with this female and referred them provisionally to this species. The two males in this series are in such poor condition that I am unable to determine whether they belong to this species or not; therefore, the male of this species remains unknown.

Type: Female, Falls Church, Virginia, Sept. 27, 1917, ex *Cucullia* sp., Type No. 43050, U. S. National Museum.

Hosts: Noctuidae: *Cucullia* sp. (1). Notodontidae: *Datana angusi* (1) and *Dasylophia anguina* (2).

Distribution: Maine westward to Manitoba, southward to Florida and southwestward to Arkansas. *Manitoba:* Aweme. *Arkansas:* Washington Co. *Florida:* Plant City. *Maine:* Baxter State Park. *Maryland:* Chesapeake Beach and Plummer Island. *Massachusetts:* Melrose Highlands. *Minnesota:* Olmstead Co. *Mississippi:* Agricultural and Mechanical College. *New Jersey:* Somerville. *New York:* Babylon, Long Island; Baiting Hollow, Long Island; Maybrook and Wading River, Long Island. *Virginia:* Falls Church.

Flight records: North of the 38th parallel this species has been taken from June through September.

Lespesia datanarum (Townsend), new combination

FIGURES 8, 20, 29

Masicera datanarum Townsend, 1892, p. 287.
Achaetoneura frenchii (in part), Webber, 1930, p. 7 (new synonymy).
Achaetoneura anisotae Webber, 1930, p. 13 (new synonymy).

A large-sized species, over-all length about 12 mm. Distinguished from all other species of the genus except *schizurae* by its large size; distinguished from *schizurae* by the presence of median marginal bristles on abdominal terga 2 and 3.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose with a faint yellowish cast. Second antennal segment black with a reddish tinge; third antennal segment black, reddish only at extreme base. Arista thickened on basal half, tapered rapidly apically. Frontal bristles about nine in number, extending to well below base of third antennal segment. Inner vertical bristles strong; outer verticals weak, about one-fourth size of inner verticals. Parafrontals with an irregular row of large black hairs outside frontal row, none of which is equal in size to bristles of the frontal row. Facial ridges bristled about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row irregular. Beard moderately thick, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Legs black, shining; with no trace of pollen except for posterior surface of front femur. Pulvilli of front tarsi about as long as last tarsal segment. Middle tibiae with one strong antero-dorsal bristle near middle and another about one-half size of strongest. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color; terga 2 to 4 gray-pollinose without a yellowish tinge, tergum 5 gray-pollinose with a definite yellowish tinge; sometimes a red spot present laterally on tergum 3, which may extend to terga 2 and 4. Terga 2 and 3 each with a strong pair of median marginal bristles, tergum 4 with a strong marginal row of bristles, tergum 5 covered with erect hairs and an irregular row of bristles near apex. Terminalia (Fig. 8) distinctive; cerci and surstyli extremely long and slender.

Female: Second antennal segment sometimes more reddish at

base than male; pulvilli of front tarsi shorter than last tarsal segment; tarsi thickened in individuals bred from *Anisota senatoria* but not thickened in individuals bred from *Datana* spp. Postabdomen (Figs. 20 and 29) distinctive, in lateral view venter of eighth sternite concave. Otherwise similar to male.

Webber, at the time of his revision, determined a series of specimens reared from *Datana integerrima* and *D. ministra* as *Achaetoneura frenchii.* A re-examination of these specimens reveals that they are very close to *datanarum.* They are similar in size, general habitus, structure of the male terminalia, the female postabdomen and other characters. The only consistent difference that is apparent is that the front tarsi of the females are not thickened in the specimens bred from *Datana* spp., whereas the front tarsi are always thickened in females bred from *Anisota senatoria.* Therefore, it seems best to regard the form which breeds on *Datana* spp. as *datanarum* rather than *frenchii.*

Measurements: See Tables I and II.

Types: Townsend (1892) described *Masicera datanarum* from four specimens without designating a holotype; two from Ithaca, New York, June 19 and 21 (no year), ex *Datana* sp., J. H. Comstock, one from Ottawa, Ontario, Canada, June 14 (no year), ex *Antheraea polyphemus,* W. Hague Harrington, and one collected specimen from Minnesota (Lugger). Of these original four, two have been located at The University of Kansas. In my opinion, two distinct species are represented in this syntypic series. A female from Ithaca, New York, June 19, is designated as lectotype of *Masicera datanarum.* The other remaining specimen, a female, is from Ottawa, Ontario, and is designated as holotype of *Lespesia sabroskyi,* new species (see p. 666).

Hosts: Arctiidae: *Diacrisia virginica.*[1] Citheroniidae: *Anisota rubicunda* (7), *A. senatoria* (66), *A. virginiensis* (11), and *Anisota* sp. (2). Notodontidae: *Datana integerrima* (18) and *D. ministra* (45).

Distribution: British Columbia to Quebec, southward to Florida and westward to California. *British Columbia:* Annis; Lavington and Mara Lake. *Manitoba:* Morden; Thornhill and Seddons Corner. *Ontario:* Belleville; Gordon Lake; Manitoulin Island; Petawawa; Stonecliff and West Bay. *Quebec:* Berthierville. *Arizona:* Paradise. *California:* Placer Co. *Connecticut:* Cromwell; Daniel-

1. This record taken from Webber (1930). I have not been able to verify it.

son; Deep River; Mystic; Preston and Putnam. *District of Columbia. Florida:* Gainesville; Monticello and Olena State Park. *Georgia:* Clayton and Pomona. *Illinois:* Forest Park and White Pine. *Indiana:* Brooksville. *Kansas. Minnesota. Missouri:* Kansas City. *New Jersey:* Franklin Park; Green Village; Kingston; Lucaston; New Brunswick and Whitesville. *New Mexico:* Jemez Springs and White Sands. *New York:* Alexandria; Baiting Hollow, Long Island; Elmira; Horseheads; Lawrenceville; Oswego; Reynoldsville and Watchogue. *Pennsylvania:* Montgomeryville and Quakertown. *Rhode Island:* Westerly. *South Carolina:* Clemson College. *Texas:* College Station. *Virginia:* Virginia Beach.

Flight records: North of the 38th parallel, this species appears to be most common during June and July.

Lespesia dimmocki (Webber), new combination

Achaetoneura dimmocki Webber, 1930, p. 20.

A medium-sized species, over-all length 7 to 9 mm. The females are easily distinguished from all other species by the longitudinal row of erect hairs that extend along the mid-dorsal line of the abdomen and stand out in sharp contrast to the adjacent depressed hairs. The males are recognized by the presence of two or more strong antero-dorsal bristles on the middle tibiae.

Male: Eyes with distinct pubescence visible at high magnification. Face and front gray-pollinose, front usually with a yellowish cast. Second antennal segment reddish brown, third antennal segment black. Arista thickened on basal two-thirds, tapering rapidly apically. Frontal bristles about eight in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals weak. Parafrontals with a regular row of bristles outside frontal row which sometimes are as large as one-half size of bristles of frontal row. Facial ridges bristled weakly about one-half distance from vibrissae to antennal bases, bristles widely and irregularly spaced. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row very irregular, scarcely discernible. Beard thin, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three lateral scutellar bristles. Apical scutellar bristles long, erect and cruciate. Legs black with a slight reddish tinge, without pollen except for posterior

surface of front femur. Pulvilli of front tarsi about as long as last tarsal segment. Middle tibiae with 2 to 5 strong antero-dorsal bristles near middle. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color, gray-pollinose without a yellowish cast except on tergum 5. Sometimes a bare red spot is present laterally on tergum 3. Terga 2 and 3 each with one pair of strong median marginal bristles; tergum 4 with a strong marginal row; tergum 5 bristled on entire surface, the bristles not in rows. Terminalia not examined.

Female: Inner vertical bristles strong, outer verticals about one-half size of inner verticals; abdomen with a longitudinal row of erect hairs extending along midline of dorsum, which stand out in sharp contrast to the adjacent depressed hairs. Otherwise similar to male.

Types: Holotype, male, Springfield, Massachusetts, June 5, 1898, G. Dimmock no. 1346a, Type No. 43051, U. S. National Museum. Allotype, female, same data as holotype. Paratypes, one male and two females, same data as holotype; one male and two females, Tatham, Massachusetts, July 15, G. Dimmock Nos. 1516b-d, ex *Automeris io.*

Hosts: Noctuidae: *Simyra henrici* (1). Saturniidae: *Automeris io* (3).

Distribution: Manitoba: Aweme. *Quebec:* Chateauguay. *Maryland:* Plummer Island. *Massachusetts:* Springfield and Tatham. *Ohio:* Columbus. *Pennsylvania:* Philadelphia.

Flight records: This species has been taken from May through August.

Lespesia euchaetiae (Webber), new combination

Figures 12, 25, 31, 34A-B

Achaetoneura euchaetiae Webber, 1930, p. 11.

A medium large-sized species, over-all length about 10 mm. It is most readily distinguished from all other species by the location of the posterior spiracles of the puparium, which are always located well above the horizontal axis (Fig. 34A). In all other species, the posterior spiracles are located on or near the horizontal axis. In the absence of a puparium, the males may be recognized by their distinctive terminalia (Fig. 12). The females can be easily confused with those of *ciliata*, but they may be separated by their longer and more attenuated postabdomen (Figs. 25, 31 and 23, 30). The fe-

males may be separated from females of the *frenchii* complex by the front which is wider at the vertex in relation to the head width (see Table II).

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, the latter with a yellowish cast. Second antennal segment black with a reddish tinge, third antennal segment black except at extreme base. Arista thickened on basal one-half, tapered rapidly apically. Frontal bristles nine to eleven in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-third size of inner verticals. Parafrontals with a regular row of bristles outside frontal row which are at most one-fourth size of bristles of frontal row. Facial ridges bristled about one-half distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row very irregular, sometimes apparently nonexistent. Beard of moderate thickness, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three to four lateral scutellar bristles, three more common. Apical scutellar bristles erect, cruciate. Legs black without a reddish tinge; without pollen except for posterior surface of front femur. Pulvilli of front tarsi about equal in length to last tarsal segment. Middle tibiae with one strong and one weak antero-dorsal bristle near middle. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color, gray-pollinose without a yellowish cast except on tergum 5. Sometimes a bare red spot present laterally on tergum 3. Terga 2 and 3 each with one strong pair of median marginal bristles; tergum 4 with a strong marginal row; tergum 5 irregularly bristled on entire surface but with bristles strongest on apical half. Terminalia (Fig. 12) distinctive; cerci and surstyli short and broad, cerci with a concavity on their posterior edge.

Female: Pulvilli of front tarsi shorter than last tarsal segment; postabdomen long and attenuated (Figs. 25 and 31). Otherwise similar to male.

Measurements: See Tables I and II.

Types: Holotype, male, Redwood, New York, July 18, 1927, Gip. Moth Lab. 12130M9, ex *Euchaetias egle,* Type No. 43047, U. S. National Museum. Allotype, female, Hingham, Massachusetts, July

24, 1925, Gip. Moth Lab. 12130115, ex *Euchaetias egle*. According to Webber (1930, p. 12), 23 paratypes were included in the original type series but none of these can now be located in the U. S. National Museum.

Hosts: Arctiidae: *Euchaetias egle* (224) and *Halisidota tessellaris*.[1]

Distribution: From southern Ontario southward to Kansas and from New England westward to South Dakota. *Ontario:* Cobden. *Connecticut:* Manchester; Pomfret; Putnam; Thompson; Willimantic and Woodstock. *Kansas:* Lawrence. *Massachusetts:* Dover; Hingham; Holliston and Sherborn. *New Hampshire:* Pelham. *New Jersey:* Bernardsville; Bridgewater; Clinton; Cranbury; Glen Gardner; Liberty Corners; North Branch; Plunkemin; Ringoes; Schooleys Mountain; Somerville and Stirling. *New York:* Adams; Bergen; Campbell; Chemung; Cortland; Crown Point; Dansville; Dekalb; Edwardsville; Elmira; Fulton; Geneva; Ithaca; Leyden; Mycenae; Natural Bridge; Newburgh; Pierrepont; Redwood; Saratoga Springs; Waverly and Wayland. *Pennsylvania:* Dingmans Ferry; Glendale; Milford; Rush; Sellersville; Tunkhannock and Whitemarsh. *South Dakota:* Big Stone City.

Flight records: This species appears to be most abundant during July.

Lespesia fasciagaster, n. sp.

A medium-sized species, over-all length about 8 mm. Distinguished from all other species of the genus except *parva* by the distinct black transverse bands on the abdominal terga and from *parva* by its larger size.

Female: Eyes bare. Face, front, and posterior surface of head silvery-pollinose. Second antennal segment red; third antennal segment red on proximal half, black on distal half. Arista thickened on basal two-thirds, tapered rapidly on distal third. Frontal bristles usually nine in number, extending to just below base of third antennal segment. Parafrontals with scattered black hairs outside frontal row, none of which is equal in size to bristles of frontal row. Facial ridges bristled for about two-thirds distance from vibrissae to antennal bases, bristles in a double row. Frontal vitta reddish brown, about one-third width of front. Bristles of occipital fringe in a double row. Beard thin, composed of white hairs.

Thorax heavily gray-pollinose with a very faint yellowish cast

1. This record taken from Webber (1930). I have not been able to verify it.

on some specimens. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a very slight reddish tinge. Middle tibiae with one strong antero-dorsal bristle. Hind tibiae ciliate with one longer bristle near middle, bristles rather widely spaced.

Abdomen black in ground color and heavily gray-pollinose with no yellowish cast on any segment. Second tergum black; terga 3 to 5 with prominent black bands on posterior margins. Terga 2 and 3 each with a strong pair of median marginal bristles; tergum 4 with a strong marginal row of widely spaced bristles; tergum 5 bare on proximal two-thirds followed by a transverse row of bristles, distal one-third of segment irregularly bristled. Postabdomen similar to that of *frenchii*.

Male: Unknown.

Measurements: See Table II.

Holotype: Female, College Station, Texas, October 4, 1921, H. J. Reinhard.

Paratypes: Three females, College Station, Texas, July 10, 1918, October 2, 1921, and April 18, 1935, H. J. Reinhard; one female, Bexar Co., Texas, September 26, 1931, H. J. Reinhard; one female, Sanford, Florida, August 4, 1930, J. Nottingham.

The holotype has been deposited in the U. S. National Museum. Two paratypes have been placed in the Snow Entomological Museum, The University of Kansas and three have been sent to Professor H. J. Reinhard at Texas Agricultural and Mechanical College.

Hosts: Unknown.

Lespesia ferruginea (Reinhard), new combination

Frontina ferruginea Reinhard, 1924, p. 269.
Achaetoneura ferruginea, Webber, 1930, p. 33.

A small and easily recognized species, over-all length 5 to 7 mm. Separated from all other species except *rileyi* and *testacea* by the extensive red areas on the abdomen and from *rileyi* and *testacea* by the presence of three lateral scutellar bristles rather than four.

Male: Eyes almost completely bare, with practically no pubescence visible at high magnification. Face and front gray-pollinose, front with a faint yellowish cast. Second antennal segment reddish brown, third antennal segment black. Arista thickened on basal half, tapered rapidly apically. Parafrontals with scattered black hairs outside frontal row none of which is equal in size to bristles of frontal row. Facial ridges bristled about two-thirds distance from

vibrissae to antennal bases, bristles rather widely spaced. Frontal vitta brown, about one-third width of front.

Thorax black in ground color, thickly gray-pollinose with a yellowish cast. Mesonotum with four well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three lateral scutellar bristles. Legs black with a yellowish tinge, without pollen except for posterior surface of front femur. Pulvilli of front tarsi shorter than last tarsal segment. Middle tibiae with one strong antero-dorsal bristle near middle and another about one-half size of strong bristle. Hind tibiae evenly ciliate with one longer bristle.

Abdomen red with the exception of a longitudinal black band extending down mid-line of dorsum, without pollen except for narrow bands on anterior margins of terga 3 to 5. Terga 2 and 3 each with one pair of median marginal bristles; tergum 4 with a marginal row; tergum 5 with a submarginal row of bristles near apex. Terminalia not seen by me.

Female: Third antennal segment more reddish on basal half; pulvilli of front tarsi about as long as last tarsal segment; postabdomen not seen. Otherwise similar to male.

Types: Holotype, male, College Station, Texas, Sept. 29, 1920, H. J. Reinhard, Type No. 27577, U. S. National Museum. Paratype, female, same data as holotype except that the collection date is July 11, 1920. The remainder of the type series of five males and two females is in the collection of H. J. Reinhard.

Hosts: Unknown.

Distribution: College Station, Texas. As far as I know, no additional specimens have been found since the species was described.

Lespesia flavifrons, n. sp.

Over-all length about 9 mm. Distinguished from all other species of the genus except *texana* by the golden-pollinose face and front and from *texana* by the facial depression which is silvery-gray instead of golden.

Male: Eyes with slight pubescence visible at high magnification. Face and front distinctly golden-pollinose; posterior surface of head silvery-pollinose. Facial depression silvery gray-pollinose. Antennae black except for extreme base of third segment which is red. Arista thickened on basal half, tapered rapidly apically. Frontal bristles about nine in number, extending to below base of third antennal segment. Inner vertical bristles strong, outer verticals

absent. Parafrontals with scattered black hairs outside frontal row, none of which is equal in size to bristles of frontal row. Facial ridges bristled about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta dark brown, about one-third width of front. Bristles of occipital fringe in a double row; posterior row irregular, composed of widely spaced bristles. Beard thick, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three to four lateral scutellar bristles. Legs black with no pollen except for posterior surface of front femur. Middle tibiae with one strong antero-dorsal bristle and another about one-half size of strongest. Hind tibiae ciliate with one longer bristle near middle.

Abdomen black in ground color; terga 2 to 4 gray-pollinose without a yellowish tinge, tergum 5 gray-pollinose with a definite yellowish tinge. Terga 2 and 3 each with a strong pair of median marginal bristles; tergum 4 with a marginal row of bristles; tergum 5 with bristles irregularly scattered over entire surface. Terminalia not distinctive, similar to those of *frenchii*.

Female: Face and front bright golden-pollinose. Third antennal segment red, second segment black. Inner vertical bristles strong, outer vertical bristles about one-half size of inner verticals. Post-abdomen distinctive, short and broad. Otherwise similar to male.

Measurements: See Tables I and II.

Holotype: Male, Melrose Highlands, Massachusetts, emerged June 1, 1931, from *Paonias myops* S. & A., C. Griswold.

Allotype: Female, Melrose Highlands, Massachusetts, emerged June 5, 1931, from *Smerinthus jamaicensis* Say, Griswold and Baker.

Paratypes: Four males, Melrose Highlands, Massachusetts, emerged June 1-2, 1931, from *Paonias myops* S. & A., C. Griswold; two males, Stroudsburg, Pennsylvania, emerged Sept. 11, 1929, from *Paonias myops* S. & A.; two females, Stroudsburg, Pennsylvania, emerged Sept. 17, 1929, from *Paonias myops* S. & A.; six females and one male, Melrose Highlands, Massachusetts, emerged Oct. 17, 1930, from *Smerinthus jamaicensis* Say, C. Griswold; one male and one female, Melrose Highlands, Massachusetts, emerged Oct. 10, 1930, from *S. jamaicensis*, C. Griswold; one female, Lafayette, Indiana. Sept. 16, 1917, J. M. Aldrich; one female, Washington, District of Columbia, H. G. Dyar; one female, Blackjack Creek, Pottawatomie

Co., Kansas, July 9, 1951, H. E. Evans; one female, Medora, Kansas, June 24, 1936, M. B. Jackson. The entire type series is in the U. S. National Museum.

Hosts: Sphingidae: *Paonias myops* (9), *Smerinthus cerisyi* (9), *Smerinthus jamaicensis* (10) and *Smerinthus* sp. (12).

Distribution: From British Columbia eastward to Newfoundland, southward to the District of Columbia. In addition to the type series, specimens have been examined from the following localities. *Alberta:* Elk Island Park and Irma. *British Columbia:* Mile 51, Big Bend Highway; Bigmouth Creek and Princeton. *Newfoundland:* Hamber. *Ohio:* Sugar Grove.

Flight records: On the basis of the limited material available, this species appears to be most common during September and October.

Lespesia frenchii (Williston)

Figures 3, 13, 32, 33

Masicera frenchii Williston, 1889, p. 1923.
Achaetoneura hesperus Brauer and Bergenstamm, 1891, p. 334.
Masicera sphingivora Townsend, 1892, p. 286.
Frontina malacosomae Curran, 1925, p. 155.
Frontina sordida Curran, 1926, p. 171, new name for *malacosomae* Curran, preoccupied.
Achaetoneura frenchii, Webber, 1930, p. 7.
Lespesia frenchii, Herting, 1960, p. 76.

It appears that several distinct species have heretofore been included under this name, and an attempt has been made to separate and describe them in this revision.

A medium-sized species, over-all length 7 to 8 mm. Distinguished from all other species by the form of the male terminalia, which are unusually small relative to the body size with short cerci and surstyli (Fig. 13) and by the characters given in the key.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose with a slight yellowish cast. Second and third antennal segments black. Arista thickened on basal one-half, tapered rapidly apically. Frontal bristles six to eight in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals very weak, scarcely differentiated from adjacent hairs of occipital fringe. Parafrontals thickly haired outside frontal row, none of hairs equal in size to bristles of frontal row. Facial ridges bristled about three-fourths distance from vibrissae to antennal bases. Frontal vitta brown, about one-

third width of front. Bristles of occipital fringe in a double row, posterior row very irregular. Beard of moderate thickness, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three to four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black, without pollen except for posterior surface of front femur. Pulvilli of front tarsi about as long as last two tarsal segments together. Middle tibiae with one strong antero-dorsal bristle near middle, sometimes another bristle is present which is always less than one-half the size of strong bristle. Hind tibiae ciliate with one longer bristle.

Abdomen black in ground color; gray-pollinose without a yellowish cast except on tergum 5; usually with a bare red spot laterally on tergum 3. Terga 2 and 3 each with one pair of median marginal bristles; fourth tergum with a marginal row; fifth tergum irregularly bristled on entire surface. Terminalia smaller relative to size of fly than in other species (Fig. 13). Cerci and surstyli short and broad; subequal to each other in length and width.

Female: Third antennal segment reddish on basal half; outer vertical bristles stronger, about one-half size of inner verticals; pulvilli of front tarsi shorter than last tarsal segment. Otherwise similar to male.

Measurements: See Tables I and II.

Types: Williston (1889) described the species from five specimens from Moosehead Lake, Maine, November 26, 1881, ex *Papilio* (= *Jasoniades*) *glaucus,* S. H. Scudder. Of these five, one male still exists in the Museum of Comparative Zoology at Harvard University, and this specimen is here designated as lectotype. It is dated Nov. 15, 1881, instead of Nov. 26 as stated by Williston. The abdomen is broken off but the remainder of the specimen is in good condition.

Hosts: Lasiocampidae: *Malacosoma americana* (192), *M. disstria* (192), *M. disstria erosa* (5), *M. fragilis* (5), *M. pluvialis* (7) and *Malacosoma* sp. (14). Lymantriidae: *Stilpnotia salicis* (1). Papilionidae: *Papilio bairdii oregonia* (2), *P. daunus* (10), *P. eurymedon* (7), *P. glaucus* (1), *P. glaucus canadensis* (1), *P. glaucus turnus* (2), *P. rutulus* (18) and *Papilio* sp. (5). Sphingidae: *Ceratomia amyntor* (11), *C. catalpae* (1), *C. undulosa* (269), *Sphinx chersis* (21) and *S. kalmiae* (4).

Distribution: From British Columbia eastward to Nova Scotia, southward to Florida and westward to California, Oregon and Washington. *Alberta:* Edmonton and Lacombe. *British Columbia:* Royal Oak and Victoria. *Manitoba:* Aweme and Whiteshell Forest. *New Brunswick:* Fredricton; Harcourt; Kent Co.; Rest and York Co. *Nova Scotia:* Annapolis; Coldbrook; Kings Co. and Truro. *Ontario:* Cameron Lake; Dorset; Emo; Franz; Galt; Greely; Jamot; Kapuskasing; Little Rapids; MacLennan township, Sudbury District; Milford Bay; Port Carling; Port Arthur; Ridgetown; Rousseau; Scadding township; Sellers; Senneterre; Simcoe; Sowerbu; Sudbury and West Ferris. *Quebec:* Kenogami; Laniel; River Turgeon and Senneterre. *Saskatchewan:* Glaslyn and Wood Mountain. *Arizona:* Sitgreaves National Forest. *California:* Berkeley; Blue Canyon; Mt. Shasta, Siskiyou Co.; Oakland; Placer Co.; Sonoma Co.; Truckee and 4 mi. S. Weed, Siskiyou Co. *Colorado:* Denver and Estes Park. *Connecticut:* Mansfield and Manchester. *District of Columbia:* Washington. *Florida:* Croom. *Illinois:* Carlinville. *Maine:* Augusta; Bath and Waldoboro. *Maryland:* Boonsboro. *Massachusetts:* Cheshire; Gloucester; Harwich; Melrose Highlands; Saugus; Sharon and Wilmington. *Minnesota:* Cass Co. and Star Island. *Montana:* Bozeman. *New Hampshire:* Milford. *New Jersey:* Cranbury; Green Village; Princeton and Somerville. *New York:* Auburn; Babylon, Long Island; Garrison; Ithaca; Leyden and Watkins. *Oregon:* Astoria; 20 mi. E. Chemult, Klamath Co.; Corvallis; Millican and Steens Mountains. *Rhode Island:* Johnston. *South Carolina. Vermont:* Newfane. *Washington:* Wenatchee.

Flight records: North of the 38th parallel this species is very abundant in July and again in September so that there may be two broods. South of the 38th parallel records extend throughout the winter.

Lespesia laniiferae (Webber), new combination

Achaetoneura laniiferae Webber, 1930, p. 33; Patton, 1958, p. 32.

A medium-sized species, over-all length 8 to 9 mm. It is distinguished by the characters given in the key.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, both with a pronounced yellowish cast. Second antennal segment reddish-yellow; third antennal segment black with a reddish tinge on basal one-third. Arista more or less uniformly tapered from base to apex, somewhat thickened on basal one-third. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles

strong, outer verticals very weak. Parafrontals with a row of bristles outside frontal row which are about one-half size of largest frontals. Facial ridges bristled about one-half distance from vibrissae to antennal bases. Frontal vitta brown, about one-third width of front.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black, lightly covered with gray pollen. Middle tibiae with one strong antero-dorsal bristle near middle. Hind tibiae evenly ciliate without a longer bristle.

Abdomen black in ground color, gray-pollinose with a yellowish cast. Tergum 2 without median marginal bristles; tergum 3 with one pair of weak median marginal bristles; tergum 4 with a marginal row of bristles; tergum 5 bristled on entire surface but with a row of stronger bristles near apex. Terminalia not seen by me.

Female: Similar to male.

Types: Holotype, male, labelled "Mexico, U. S. A., May 1927, ex *Laniifera cyclades*, Type No. 43056, U. S. National Museum." Allotype, female, same data as type. The locality label of "Mexico, U. S. A." is paradoxical and I am not clear as to what the collector meant by it. The host, *Laniifera cyclades* (Druce) (*Pachynoa cyclades* Druce, Biologia Centrali-Americana, Lepidoptera-Heterocera, 2:220) was described from specimens from Durango City and Mexico City, Mexico. Thus it appears that the type specimens of *Lespesia laniiferae* originated somewhere in Mexico. Webber (1930) gave the type locality as Mexico and I am unable to pinpoint it further.

Host: Pyralidae: *Laniifera cyclades* (2).

Distribution: Mexico. I have found no specimens in addition to the types.

Lespesia melalophae (Allen), new combination

FIGURE 14

Achaetoneura melalophae Allen, 1926, p. 195; Webber, 1930, p. 17.

A small-sized species, over-all length 5 to 7 mm. The species is readily recognized by its slender shape, small size, deep golden pollen of face and front, mottled, yellowish gray pollination of the abdomen, which is in contrast to the more uniform sheen of the other species, and the narrow front (see Tables I and II).

Male: Eyes with slight pubescence visible at high magnification.

Face and front golden-pollinose. Second and third antennal segments black. Arista thickened on basal one-third, tapered rapidly apically. Frontal bristles about eight in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals very weak, scarcely differentiated from adjacent hairs of occipital fringe. Parafrontals with scattered black hairs outside frontal row, none of which is equal in size to bristles of frontal row. Facial ridges bristled about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row irregular. Beard of medium thickness, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four fairly well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Three lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a reddish tinge, without pollen except for posterior surface of front femur. Pulvilli of front tarsi about as long as last two tarsal segments together. Middle tibiae with one strong antero-dorsal bristle near middle, no other bristles developed. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color, yellowish gray-pollinose, tergum 3 usually without a red spot laterally. Terga 2 and 3 each with one pair of median marginal bristles; tergum 4 with a marginal row of bristles; tergum 5 with an irregular row of bristles near apex. Terminalia (Fig. 14) similar to those of *frenchii.*

Female: Third antennal segment red on basal half; pulvilli of front tarsi about as long as last tarsal segment; postabdomen not distinctive. Otherwise similar to male.

Measurements: See Tables I and II.

Types: Holotype, male, Agricultural and Mechanical College, Mississippi, Aug. 17, 1924, H. W. Allen, ex *Icthyura inclusa,* Type No. 40296, U. S. National Museum. Allotype, female, Agricultural and Mechanical College, Mississippi, ex *Icthyura inclusa.* Paratypes, one male, August 28, and one female August 29, 1921, Columbus, Ohio, H. W. Allen, ex *Icthyura inclusa.* One male, fall of 1923; one male, October 3, 1923; one female, March 16, 1924; one male, March 22, 1924; one male, March 24, 1924; one male, July 25, 1924; one male and one female, August 17, 1924; two females, August 18, 1924; one male, September 17, 1924; and two females with no date, all from Agricultural and Mechanical College, Mississippi, reared

from *Icthyura inclusa* by H. W. Allen. One male, Agricultural and Mechanical College, Mississippi, April 21, 1924, H. W. Allen, collected on foliage of peach.

Hosts: Lasiocampidae: *Malacosoma disstria* (20). Noctuidae: *Nycteola cinereana* (1). Notodontidae: *Icthyura inclusa* (301).

Distribution: British Columbia eastward to New Brunswick, southward to Mississippi and westward to Illinois. *Alberta:* Edmonton. *British Columbia:* Keremeos and Quesnel. *New Brunswick:* Green River and Victoria. *Ontario:* Algonquin Park; Brights Grove; Cochrane; Essex; Franz; Harkett; Patton; Sault St. Marie; Sellers; Temagami; Tranoga; and Valrita. *Quebec:* Magloire. *Saskatchewan:* Marsden. *Colorado:* Pagosa Springs. *Connecticut:* Fairfield; Putnam; Thompson and Woodstock. *Illinois:* Carbondale. *Mississippi:* Agricultural and Mechanical College. *Missouri:* Charleston. *New Jersey:* Bound Brook; Burlington; Flemington; Liberty Corners; North Branch; Ringoes; Somerville and Whitehouse. *Ohio:* Columbus. *Pennsylvania:* Exeter. *Rhode Island:* Westerly. *Virginia:* Backbay.

Flight records: North of the 38th parallel, this species appears to be most abundant in August. South of the 38th parallel, it is found throughout the year.

Lespesia parva, n. sp.

A small species, in fact, the smallest known species in the genus; over-all length about 5 mm. Distinguished from all other species of the genus by its small size and the distinct transverse bands on the abdomen.

Male: Eyes bare. Face, front, and posterior surface of head silvery-pollinose. Second and third antennal segments black. Arista thickened for nearly its entire length, abruptly pointed apically. Frontal bristles about eight in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-half size of inner verticals. Parafrontals with scattered black hairs outside the frontal row, none of which is equal in size to bristles of frontal row. Facial ridges bristled for about two-thirds distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row. Beard very thin, composed of a few sparse, white hairs.

Thorax heavily gray-pollinose. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in

intensity in different reflections. Three lateral scutellar bristles. Apical scutellar bristles strong, cruciate. Legs black and shining except for posterior surface of front femur which is gray-pollinose. Pulvilli of front tarsi shorter than last tarsal segment. Middle tibiae with one strong antero-dorsal bristle. Hind tibiae ciliate with one longer bristle near middle, bristles quite widely spaced.

Abdomen black in ground color and heavily gray-pollinose with no yellowish cast on any segment. Second tergum black and shining; terga 3 to 5 each with a prominent black band on posterior margin. Terga 2 and 3 each with a strong pair of median marginal bristles; tergum 4 with a strong marginal row of widely spaced bristles; tergum 5 bare on proximal two-thirds followed by a transverse row of bristles, distal one-third of segment irregularly bristled. Terminalia not examined.

Female: Second and third antennal segments reddish-yellow, otherwise similar to male.

Holotype: Male, Rodeo, New Mexico, Aug. 22, 1938, H. J. Reinhard.

Allotype: Female, Bexar Co., Texas, 1931, H. B. Parks.

Paratypes: One female, 1 mi. NE. Portal, Cochise Co., Arizona, Sept. 7, 1959, J. R. Powers; one female, 12 mi. SE. Ivanpah, San Bernardino Co., California, May 1, 1956, M. Wasbauer. The holotype and allotype have been deposited in the U. S. National Museum. The paratypes have been sent to the University of California at Berkeley.

Lespesia pholi (Webber), new combination

Figure 15

Achaetoneura pholi Webber, 1930, p. 27.

A medium-sized species, over-all length 8 to 9 mm. Easily recognized by the color of the pollen of the thorax, which has a yellowish cast visible to the naked eye.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, the latter with a bright yellowish cast. Second and third antennal segments black. Arista tapered nearly uniformly for its entire length. Frontal bristles eight to ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals very weak, scarcely differentiated from adjacent hairs of occipital fringe. Parafrontals with scattered black hairs outside frontal row none of which is equal in size to bristles of frontal row. Facial ridges bristled weakly for one-

half distance from vibrissae to antennal bases, bristles sometimes in a double row. Frontal vitta brown, about one-fourth width of front. Bristles of occipital fringe in a double row, posterior row very irregular. Beard of medium thickness, composed of white hairs.

Thorax black in ground color, gray-pollinose with a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a reddish tinge, without pollen except for posterior surface of front femur. Pulvilli of front tarsi about as long as last two tarsal segments together. Middle tibiae with one strong anterodorsal bristle near middle, usually no other bristles developed. Hind tibiae ciliate with one longer bristle near middle.

Abdomen black in ground color, lightly gray-pollinose, usually without red areas laterally on tergum 3. Median marginal bristles absent on tergum 2; present on tergum 3; fourth tergum with a marginal row; fifth tergum irregularly bristled on entire surface. Terminalia distinctive (Fig. 15), cerci with a pronounced concavity on posterior edge.

Female: Third antennal segment reddish on basal one-half; front more yellowish; pulvilli of front tarsi about as long as last tarsal segment; postabdomen not examined. Otherwise similar to male.

Types: Holotype, male, Springfield, Massachusetts, no date, G. Dimmock No. 2103, ex *Pholus* sp., Type No. 43055, U. S. National Museum. Allotype, female, same data as holotype. Paratypes, three males and ten females, same data as holotype.

Hosts: Sphingidae: *Pholus satellitia pandorus* (7) and *Pholus* sp. (15).

Distribution: In addition to the types, specimens from Antrim, Wright Co., Missouri, have been examined.

Flight records: The specimens from Antrim, Missouri, emerged in April. No dates were given for the type series.

Lespesia rileyi (Williston), new combination

FIGURES 16, 26

Masicera rileyi Williston, 1889, p. 1924.
Achaetoneura rileyi, Webber, 1930, p. 32; Patton, 1958, p. 32.

A medium-sized species, over-all length 6 to 8 mm. Easily distinguished from all other species except *ferruginea* and *testacea* by the extensive reddish areas of the abdomen and from *ferruginea* and

testacea by the absence of median marginal bristles on abdominal tergum 3.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, usually without a yellowish cast or with at most a very faint yellowish cast. Second antennal segment reddish yellow, third antennal segment black. Arista tapered nearly uniformly from base to apex. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-fourth size of inner verticals. Parafrontals with scattered hairs outside frontal row, sometimes with a row of bristles which may be as large as one-half size of bristles of frontal row. Facial ridges bristled weakly for about one-third distance from vibrissae to antennal bases, bristles in a double row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row very irregular. Beard of medium thickness, composed of white hairs.

Thorax black in ground color, gray-pollinose with a yellowish cast. Mesonotum with four fairly well-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a reddish tinge, without pollen except for posterior surface of front femur. Pulvilli of front tarsi about as long as last tarsal segment. Middle tibiae with one strong antero-dorsal bristle, no other bristles developed. Hind tibiae ciliate, usually without a longer bristle although there are a few exceptions.

Abdomen red in ground color, without pollen except for a narrow longitudinal band on mid-line of dorsum. Median marginal bristles absent on terga 2 and 3; fourth tergum with a marginal row; fifth tergum irregularly bristled on entire surface. Terminalia (Fig. 16) distinctive, cerci broader than surstyli.

Female: Pulvilli of front tarsi shorter than last tarsal segment; postabdomen (Fig. 26) distinctive, short and broad. Otherwise similar to male.

Types: Williston (1889, p. 1924) states that this species was described from "three males and four females from Dr. Riley, labeled: 153, parasitic on *Heraclides cresphontes* and 358, Feb. 24, '80." In the U. S. National Museum I located two males and six females, all of which bore code numbers resembling the above, so there is some discrepancy. None of the specimens bearing the code number 153 has a locality label except one female, and this is labeled

Crescent City, Fla. This is here accepted as the type locality. A male labeled 153a (no locality) is here designated as lectotype.

Host: Papilionidae: *Papilio cresphontes* (38).

Distribution: Southern United States from Florida westward to Texas. *Florida:* Gainesville; Miami; Orlando and Tampa. *Louisiana:* Baton Rouge. *Mississippi:* Gulfport. *Texas:* College Station; Richmond; Victoria and Willacy Co.

Flight records: The majority of the records are for October, with a lesser number for February and March.

Lespesia sabroskyi, n. sp.

FIGURES 18, 27

A large species, over-all length 10 to 12 mm. Extremely close to *callosamiae*, from which it can be separated by the form of the male terminalia (Figs. 18 and 10), the form of the female postabdomen (Figs. 27 and 22), and the host, if known. So far as is known, this species parasitizes *Antheraea polyphemus*, *Automeris io* and *Hyalophora euryalus*, whereas *L. callosamiae* parasitizes only *H. promethea*. This species is similar in size to *datanarum* from which the males may be separated by the terminalia (Figs. 18 and 8). In *datanarum*, the cerci and surstyli are longer and more slender. The females may be separated from *datanarum* by the form of the postabdomen (Figs. 27 and 20). Other species which are morphologically quite similar to *sabroskyi* such as *euchaetiae*, *ciliata*, and *frenchii*, may usually be separated from *sabroskyi* by their smaller body size.

Male: Eyes with very slight pubescence visible at high magnification. Face and front gray-pollinose, latter with a yellowish cast. Second and third antennal segments black. Arista thickened on basal one-third, tapered rapidly apically. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-half size of inner verticals. Parafrontals with scattered black hairs outside frontal row and a row of hairs, all of which are much smaller than bristles of frontal row. Facial ridges bristled for about one-half distance from vibrissae to antennal bases, bristles in a single row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row irregular. Beard of medium thickness, composed of white hairs.

Thorax gray-pollinose without a yellowish cast. Mesonotum with four well-defined black vittae visible from postero-dorsal view which

vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black and shining with a reddish tinge, with very little pollen except for posterior surface of front femur which is gray-pollinose. Pulvilli of front tarsi about as long as last two tarsal segments together. Middle tibiae with one strong antero-dorsal bristle; if other bristles are developed they are less than one-half size of the strong bristle. Hind tibiae evenly ciliate with one longer bristle near middle.

Abdomen black in ground color; gray-pollinose with a yellowish cast which is most pronounced on tergum 5. Tergum 3 often with red spots laterally. Terga 2 and 3 each with one pair of median marginal bristles; tergum 4 with a marginal row of bristles; tergum 5 with an irregular row of bristles at about two-thirds distance from base to apex. Terminalia (Fig. 18) distinctive.

Female: Third antennal segment mostly red; pulvilli of front tarsi shorter than last tarsal segment; postabdomen (Fig. 27) distinctive. Otherwise similar to male.

Measurements: See Tables I and II.

Type: Described from one female, Ottawa, Ontario, Canada, June 14 (no year), ex *Antheraea polyphemus*, W. Hague Harrington, in the Snow Entomological Museum, The University of Kansas. This specimen was included in the series from which Townsend (1892) described *Masicera datanarum* without designating a holotype. This series actually represents two species and a female from Ithaca, New York, June 19 (no year), ex *Datana* sp., J. H. Comstock, is designated as lectotype of *datanarum* (see p. 649). The remaining specimen is designated as the type of this new species.

This species is named in honor of Mr. Curtis W. Sabrosky of the United States National Museum.

Hosts: Saturniidae: *Antheraea polyphemus* (192), *Automeris io* (2), and *Hyalophora euryalus* (4).

Distribution: From British Columbia to Quebec, southward to Mississippi and westward to California and Oregon. *British Columbia:* Miles 9, 39 and 101, Big Bend Highway; Dragon Lake; Eagle Bay; Gold Stream; Green Lake; Heywood Corner; Kaslo; Mara; Mara Lake; Mission; Peachland Creek; Shuswap Lake; Trinity Valley; Vancouver and Vernon. *Manitoba:* Aweme. *Ontario:* Ignace District; Kenora District; Ottawa and Skead and Trout Lake, Algoma District. *Quebec:* Hemmingford; Laniel and Mt. Royal. *Saskatchewan:* Indian Head and Saskatoon. *California:* Mill Valley, Marin Co.; Mountain View; Patterson; San Leandro, Alameda

Co.; Shasta Springs; Sunnyvale, Santa Clara Co.; and West Pittsburg, Contra Costa Co. *Connecticut:* Manchester; New Haven and Stamford. *Massachusetts:* Melrose Highlands and Somerville. *Michigan:* Cheboygan Co. *Minnesota. Mississippi:* Agricultural and Mechanical College. *New Hampshire:* Andover. *New Jersey:* Hammonton; New Brunswick; Rutherford and Trenton. *New York:* Ithaca. *Ohio:* Bratenahl. *Oregon:* Corvallis and Eugene and vicinity. *Pennsylvania:* Harrisburg and Lansdowne. *Texas:* Austin. *Vermont:* Websterville. *Virginia:* Charlottesville.

Flight records: The records for this species are scattered throughout the year and this is probably due to the fact that many of the flies emerged from pupae which were held indoors over the winter, which apparently caused the flies to emerge earlier than they would have in nature. For example, I have many records for December, January and February in Canada. It seems highly unlikely that flies would emerge in nature at this time of year at this latitude. However, it seems most likely that this species flies at some time during the period of April through June north of the 38th parallel, since there are a number of records for these months.

Lespesia schizurae (Townsend), new combination

FIGURE 17

Masicera schizurae Townsend, 1891b, p. 187.
Sturmia schizurae Coquillett, 1897, p. 113.
Argyrophylax piperi Townsend, 1908, p. 98 (new name).
Achaetoneura schizurae, Aldrich, 1929, p. 36.
Achaetoneura piperi, Webber, 1930, p. 29 (new synonymy); Patton, 1958, p. 32.
Achaetoneura schizurae, Webber, 1930, p. 28; Patton, 1958, p. 32.

Webber (1930) regarded *piperi* as a distinct species from *schizurae* Townsend. After examining many specimens from various parts of the range, I can find no basis for maintaining the name *piperi,* and it is here treated as a synonym of *schizurae.* According to Webber, *piperi* can be distinguished from *schizurae* Townsend by its larger size and more robust form; hind tibiae of male densely ciliate without a longer bristle; fourth abdominal tergum densely bristled except at extreme base, bristles at apex strongest; facial ridges strongly bristled a little over one-half distance from vibrissae to antennal bases; front pulvilli of male smoky black, nearly as long as last two tarsal segments; whereas *schizurae* Townsend is smaller and less robust; hind tibiae of male less densely ciliate and with one longer bristle; more sparsely bristled fourth abdominal tergum; facial ridges weakly bristled one-half distance from vibrissae to antennal bases; front pulvilli of male shorter and grayish rather than

black. Additional minor characters are mentioned. None of these characters holds up in a long series of specimens because many individuals are found which combine the characters of the two nominal species. For example, many large robust males are found which have a longer bristle on the hind tibia. Furthermore, the type of *Masicera schizurae* Townsend was reared from *Schizura unicornis;* and the type of *Sturmia schizurae* Coquillet (= *Argyrophylax piperi* Townsend) was reared from *Schizura ipomoeae.* This suggests biological as well as morphological similarities between the two nominal species. Therefore, *piperi* is best regarded as a synonym of *schizurae* Townsend.

A variable-sized species, body length ranging from 8 to 12 mm. The larger males are usually similar in size to the males of *datanarum,* from which they can be distinguished by the absence of median marginal bristles on abdominal terga 2 and 3, and by the differently shaped abdomen, which is wider and more flattened than that of *datanarum.* The smaller males are difficult to distinguish from the males of *aletiae,* but they can be separated by their terminalia (see Figs. 17 and 7). The females can be distinguished from all other species of the genus except *pholi, cuculliae* and *laniiferae* by median marginal bristles which are absent on abdominal tergum 2 but present on abdominal tergum 3, and from *pholi, cuculliae* and *laniiferae* by their large size.

Male: Eyes varying from bare to slightly pubescent. Face and front gray-pollinose with a slight tinge of golden. Second and third antennal segments black. Arista tapered nearly uniformly for its entire length, thickened slightly on basal half. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals very weak. Parafrontals thickly haired outside the frontal row, none of hairs equal in size to bristles of frontal row. Facial ridges bristled for about one-half distance from vibrissae to antennal bases, bristles usually in a double row. Frontal vitta brown, about one-third width of front. Bristles of occipital fringe in a double row, posterior row very weak. Beard very thick, composed of white hairs.

Thorax lightly gray-pollinose. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate, relatively weak. Legs black and shining with a reddish tinge except for posterior surface of front femur which is gray-pollinose. Pulvilli of front tarsi about as long

as last two tarsal segments together. Middle tibiae with one strong and one weak antero-dorsal bristle. Hind tibiae densely ciliate with or without a longer bristle near middle.

Abdomen black in ground color dorsally, shading to red laterally; lightly gray-pollinose without a yellowish cast. Median marginal bristles absent on tergum 2, usually absent on tergum 3; tergum 4 with a marginal row of bristles; tergum 5 irregularly bristled at apex. Terminalia distinctive (Fig. 17).

Female: Pulvilli of front tarsi shorter than last tarsal segment; outer vertical bristles well-developed; strong median marginal bristles always present on abdominal tergum 3. Otherwise similar to male.

Measurements: See Tables I and II.

Types: Townsend originally described the species from four specimens, Manhattan, Riley County, Kansas, Oct., F. A. Marlatt, reared from *Schizura unicornis*. Of these, one male has been located at the U. S. National Museum and two males at The University of Kansas. Coquillett originally described *Sturmia schizurae* from two males and three females, Pullman, Washington, C. V. Piper, bred from *Schizura ipomoeae*. Of these, one male and two females were located at the U. S. National Museum.

Townsend (1908) placed *Sturmia schizurae* Coquillett in *Argyrophylax* Brauer and Bergenstamm. The specific name was preoccupied by *Argyrophylax schizurae* Townsend, so he gave it a new name, *piperi*. According to Walton (1916, p. 192), Townsend was mistaken in referring *schizurae* Coquillett to *Argyrophylax*. Among the principal characters of the genus *Argyrophylax* are the absence of ocellar bristles, the narrow cheeks, and weakly ciliated facial ridges. Since *schizurae* Coquillett does not have these characters, it cannot be regarded as an *Argyrophylax* and is here treated as a *Lespesia*, in which genus it is also preoccupied by *schizurae* Townsend as noted in the synonymy.

Hosts: Notodontidae: *Heterocampa biundata* (11), *Heterocampa* sp. (2), *Schizura ipomoeae* (6) and S. *unicornis* (4).

Distribution: British Columbia westward to Ontario, southward to Florida and westward to Arizona. *British Columbia:* Mara Lake and Vancouver. *Ontario:* Bala; Bells Corners; Buckhorn and Sault St. Marie. *Arizona:* Indian Creek Canyon, Chiricahua Mountains and Ruby. *Arkansas:* Ozone and Washington Co. *District of Columbia:* Washington. *Florida:* La Belle and Larkins. *Georgia. Idaho:* La Wahla. *Illinois:* Carlinville and Havana. *Kansas:* Coffey

Co.; Lawrence, and Montgomery Co. *Maryland:* Plummer Island. *Massachusetts:* Woods Hole. *Michigan:* Douglas Lake. *Missouri:* Kirkwood. *New Jersey:* Lancaster and Riverton. *New Mexico:* Koehler. *New York:* Baiting Hollow, Long Island; Canandaigua Lake; Huntingdon, Long Island; Ithaca; Riverhead, Long Island; Southampton, Long Island; Tuxedo; and Wading River, Long Island. *Ohio:* Sugar Grove. *Oklahoma:* Wichita National Forest. *Pennsylvania:* Lehigh Gap and Shamokin. *Texas:* College Station and Hidalgo Co. *Utah:* Green Canyon, Logan. *Virginia:* Dixie Ledge. *Washington:* Colfax.

Flight records: North of the 38th parallel, the majority of the records are for July, August and September. South of the 38th parallel records extend throughout the winter.

Lespesia testacea (Webber), new combination

Frontina violenta, Coquillett, 1897, p. 108 (misidentification).
Achaetoneura testacea Webber, 1930, p. 25.

A medium-sized species, length 7 to 8 mm. Distinguished from all other species except *rileyi* and *ferruginea* by the predominantly bare and red abdomen; from *rileyi* it differs by the presence of median marginal bristles on abdominal tergum 3; and from *ferruginea* by the presence of four lateral scutellar bristles instead of three as in *ferruginea*.

This species is exceedingly close to *rileyi* and perhaps should be combined with it. Only about two characters can be used to separate the two species; *i. e.*, in *rileyi* the hind tibiae are ciliate without a longer bristle and median marginal bristles are absent on abdominal tergum 3, whereas in *testacea* the hind tibiae are ciliate with a longer bristle and median marginal bristles are present on abdominal tergum 3. The male terminalia and the female postabdomen are almost exactly alike. The two characters mentioned in the preceding sentence hold in most cases but there are exceptions. Specimens are found which combine the characters of the two species. Since the two species can be separated in the majority of cases, they are here treated as distinct.

Male: Eyes with slight pubescence visible at high magnification. Face and front gray-pollinose, face with a yellowish cast. Second antennal segment black with a reddish tinge, third antennal segment black. Arista thickened on basal one-half, tapered rapidly apically. Frontal bristles about ten in number, extending to just below base of third antennal segment. Inner vertical bristles strong, outer verticals very weak, scarcely differentiated from the adjacent hairs

of occipital fringe. Parafrontals with a few scattered hairs outside the frontal row, none of which is equal in size to the bristles of frontal row. Facial ridges bristled weakly for about one-third distance from vibrissae to antennal bases. Frontal vitta brown, about one-fourth width of front. Bristles of occipital fringe in a double row, posterior row very weak and irregular. Beard of medium thickness, composed of white hairs.

Thorax gray-pollinose with a faint yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black and shining with a reddish tinge, femora very lightly gray-pollinose. Pulvilli of front tarsi about as long as last two tarsal segments together. Middle tibiae with one strong antero-dorsal bristle, no other bristles developed. Hind tibiae evenly ciliate, with one longer bristle near middle.

Abdomen red in ground color except for a longitudinal black band extending along mid-line of dorsum; without pollen except for narrow bands at anterior margins of the terga. Median marginal bristles absent on tergum 2; present on tergum 3; fourth tergum with a marginal row; fifth tergum bristled on entire surface but bristles denser on apical half. Terminalia almost exactly like those of *rileyi*.

Female: Outer vertical bristles stronger, about one-half size of inner verticals; pulvilli of front tarsi shorter than last tarsal segment; postabdomen almost exactly like that of *rileyi*.

Types: Holotype, male, Washington, District of Columbia, October 8, 1884, ex *Pholus vitis*, Type No. 43054, U. S. National Museum. Allotype, female, Washington, District of Columbia, October 8, 1884, ex Lepidoptera larva. Paratype, one male, same data as holotype. According to Webber (1930, p. 26), there were two more specimens in the original type series, but these are missing.

Hosts: Noctuidae: *Xerociris wilsoni* (1). Sphingidae: *Pholus achemon* (2) and *P. vitis* (12).

Distribution: New York southward to North Carolina, westward to Texas. In addition to the types, specimens from the following localities have been examined. *District of Columbia:* Washington. *Kansas:* Wichita. *Maryland:* Plummer Island. *New York:* Baiting Hollow, Long Island. *North Carolina:* Raleigh. *Texas:* Brownsville.

Flight records: North of the 38th parallel, the majority of the few records available are for October.

Lespesia texana (Webber), new combination

Achaetoneura texana Webber, 1930, p. 24.

A medium-sized species, over-all length 9 to 10 mm. Easily recognized by the deep golden pollen of the face, front, and facial depression. Some other species have a golden-pollinose face and front but no other species has a golden-pollinose facial depression.

Male: Eyes with slight pubescence visible at high magnification. Face, front, and facial depression deep golden-pollinose. Second and third antennal segments black. Arista thickened on basal one-half, tapering rapidly apically. Frontal bristles about eight in number, extending to below base of third antennal segment. Inner vertical bristles strong, outer verticals about one-third size of inner verticals. Parafrontals often with a row of hairs outside frontal row which may be as large as one-third size of bristles of frontal row. Facial ridges bristled from one-third to two-thirds distance from vibrissae to antennal bases. Frontal vitta brown, about one-fourth width of front.

Thorax black in ground color, gray-pollinose with a yellowish cast. Mesonotum with four poorly-defined black vittae visible from postero-dorsal view which vary in intensity in different reflections. Four lateral scutellar bristles. Apical scutellar bristles erect, cruciate. Legs black with a faint yellowish tinge, thinly gray-pollinose. Middle tibiae with one strong antero-dorsal bristle near middle, no other bristles developed. Hind tibiae evenly ciliate with one longer bristle.

Abdomen black in ground color, gray-pollinose with a yellowish cast. Terga 2 and 3 each with one pair of median marginal bristles; tergum 4 with a marginal row of bristles; fifth tergum with an irregular row of bristles near apex. Fifth tergum bright golden-pollinose. Terminalia not seen.

Female: Third antennal segment more reddish, reddish on basal one-half. Otherwise similar to male.

Types: Holotype, male, Dilley, Texas, LI, 1924, Type No. 43052, U. S. National Museum. Allotype, female, Distrito Federal, Mexico, L. Conradi.

Hosts: Unknown.

Distribution: Mexico: Distrito Federal. *Texas:* Dilley.

SPECIES NOT OTHERWISE ACCOUNTED FOR WHICH WERE REFERRED TO *LESPESIA* (= *ACHAETONEURA*) BY WEBBER (1930)

spectabilis (Aldrich). *Frontina spectabilis* Aldrich, 1916, p. 21. Brooks (1945) erected a new genus, *Eufrontina*, for this species and I am in accord with this view.

westonia Webber. *Achaetoneura westonia* Webber, 1930, p. 24. This species was described from a single specimen which is in extremely poor condition. I suspect it to be an *archippivora* but can't be sure because of the condition of the type.

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TABLE 1.—Summary of Measurements Taken from the Males of the Most Common Species of *Lespesia*.

SPECIES	N	Head width		Frontal width at vertex		*Ratio		r-m to tip of $R_4 + 5$	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
aletiae	28	2.83	.220	.72	.063	.254	.0092	3.32	.310
anisotae	23	3.41	.786	1.14	.018	.335	.0146	3.66	.277
archippivora	30	2.48	.198	.97	.084	.393	.0126	.....	.....
callosamiae	25	3.12	.182	.99	.052	.316	.0101	3.41	.213
ciliata	25	2.93	.057	1.06	.033	.360	.0091	3.08	.076
euchaetiae	25	3.25	.119	1.11	.058	.340	.0113	3.24	.349
flavifrons	7	2.84	.296	.95	.105	.335	.0068	3.16	.271
frenchii	25	2.85	.091	.91	.030	.319	.0111	.....	.....
melalophae	25	2.35	.203	.67	.061	.285	.0150	2.74	.538
sabroskyi	23	3.17	.153	.98	.069	.309	.0154	3.48	.268
schizurae	35	3.43	.249	.94	.084	.274	.0187	4.25	.414

* Ratio = Frontal width at vertex/head width.

TABLE 2.—Summary of Measurements Taken from the Females of the Most Common Species of *Lespesia*.

SPECIES	N	Head width		Frontal width at vertex		*Ratio		r-m to tip of $R_4 + 5$	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
aletiae	26	2.97	.255	.84	.081	.284	.0084	3.28	.302
anisotae	32	3.56	.301	1.24	.098	.347	.0130	3.78	.330
archippivora	25	2.73	.283	1.05	.104	.408	.0112	.....	.....
callosamiae	11	3.13	.450	1.04	.150	.331	.0126	3.39	.436
ciliata	25	2.94	.136	1.25	.137	.376	.0149	3.13	.200
euchaetiae	25	3.34	.207	1.07	.125	.366	.0124	3.19	.182
fasciagaster	6	3.01	.156	1.20	.061	.398	.0125	2.81	.021
flavifrons	11	2.86	.218	.97	.108	.338	.0194	3.13	.226
frenchii	25	2.99	.103	1.00	.050	.380	.0137	.....	.....
melalophae	25	2.41	.142	.73	.062	.303	.0173	2.94	.649
sabroskyi	25	3.32	.172	1.09	.068	.328	.0118	3.53	.253
schizurae	33	3.51	.191	1.09	.100	.309	.0188	3.96	.193

* Ratio = Frontal width at vertex/head width.

FIGURES 1-6

FIGURE 1.—Anterior view of head. The arrow indicates the measurement of head width.

FIGURE 2.—Dorsal view of head. The arrow indicates the measurement of frontal width at vertex.

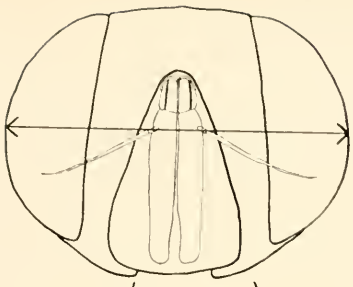
FIGURE 3.—Anterior view of head of male of *Lespesia frenchii.*

FIGURE 4.—Anterior view of head of male of *Lespesia archippivora.*

FIGURE 5.—Anterior view of head of female of *Lespesia archippivora.*

FIGURE 6.—Left lateral view of head of female of *Lespesia archippivora.*

FIGURES 1-6



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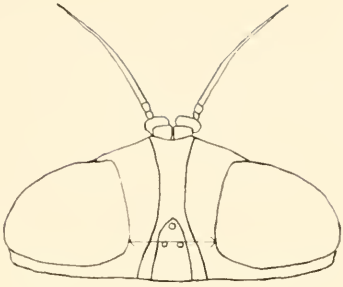

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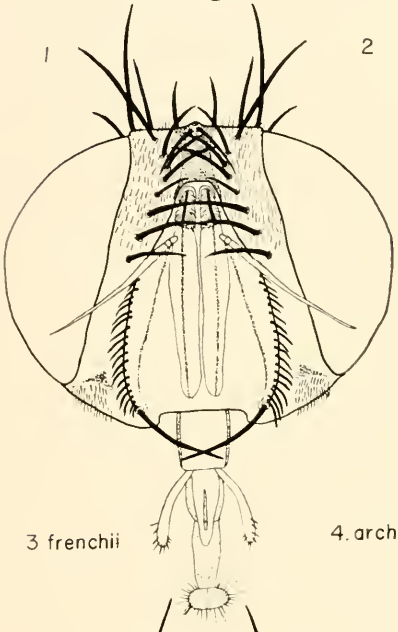
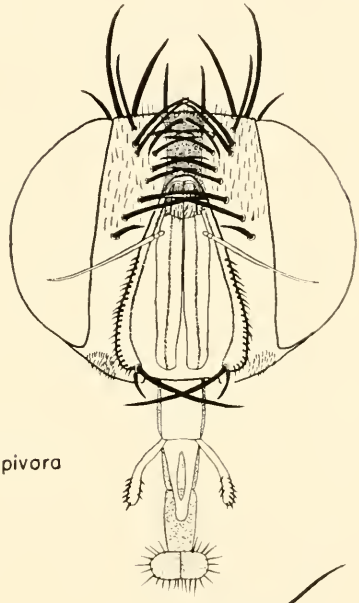
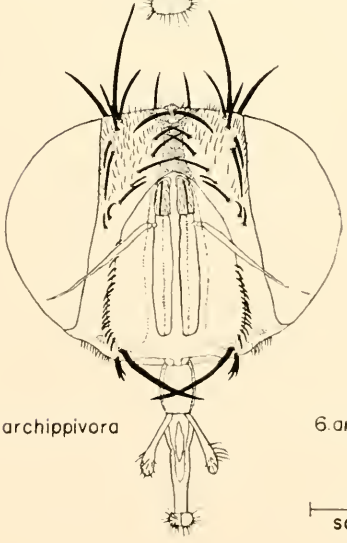


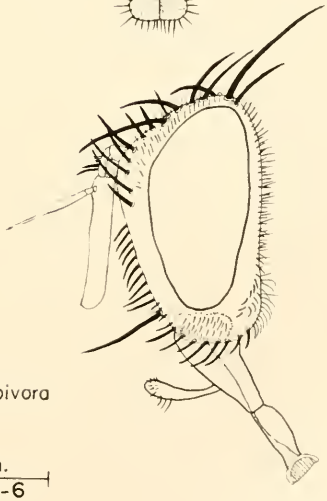
3 frenchii



4. archippivora



5 archippivora



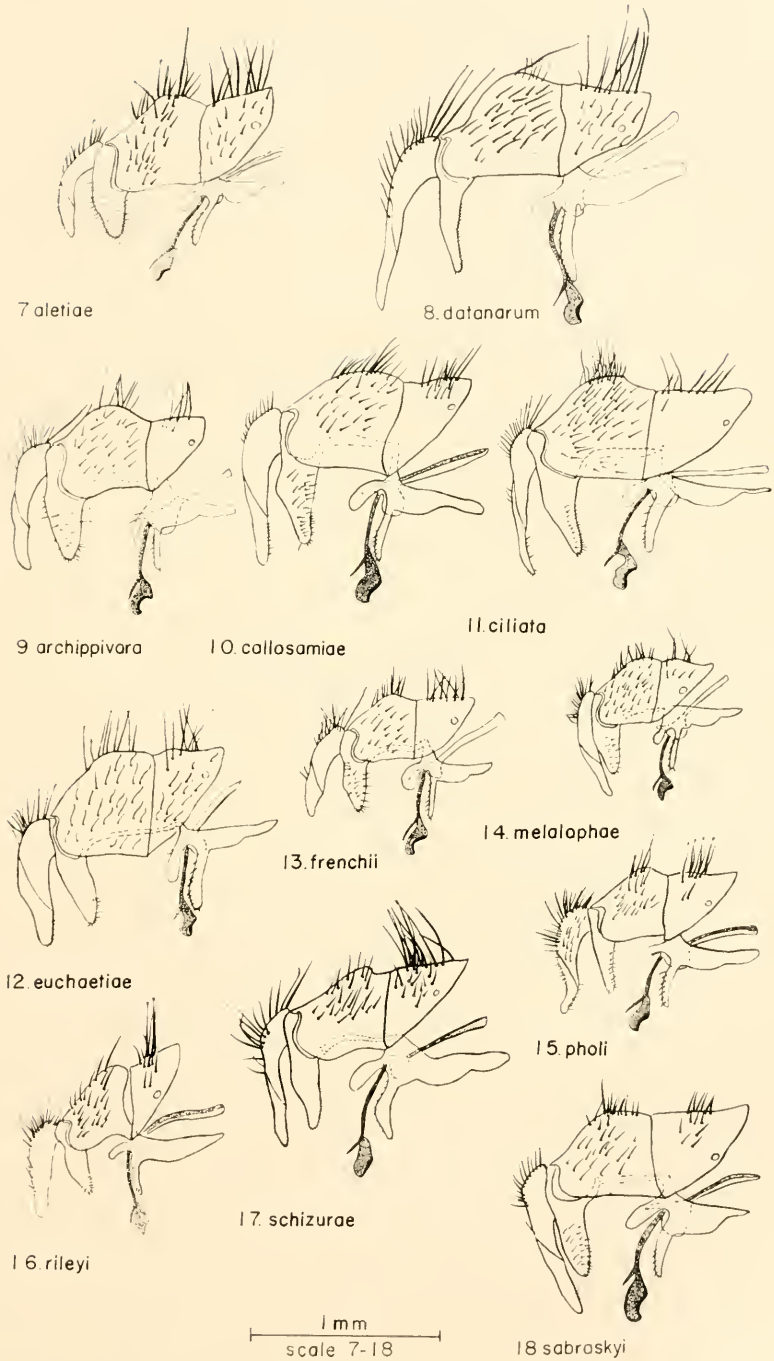
6. archippivora

1 mm.
scale: 1-6

FIGURES 7-18

FIGURES 7-18.—Right lateral views of terminalia of males of *Lespesia*. 7. *aletiae*; 8. *datanarum*; 9. *archippivora*; 10. *callosamiae*; 11. *ciliata*; 12. *euchaetiae*; 13. *frenchii*; 14. *melalophae*; 15. *pholi*; 16. *rileyi*; 17. *schizurae*; 18. *sabroskyi*.

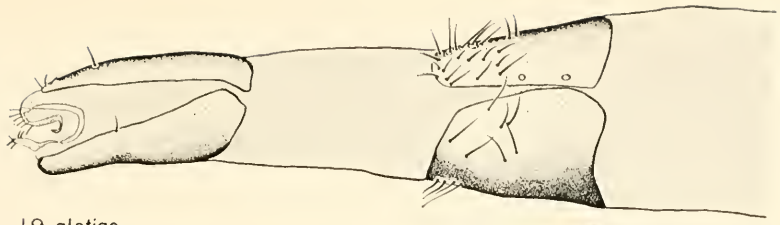
FIGURES 7-18


7. aletiae
8. datanarum
9. archippivora
10. callosamiae
11. ciliata
12. euchaetiae
13. frenchii
14. melalophae
15. pholi
16. rileyi
17. schizurae
18. sabraskyi
1 mm
scale 7-18

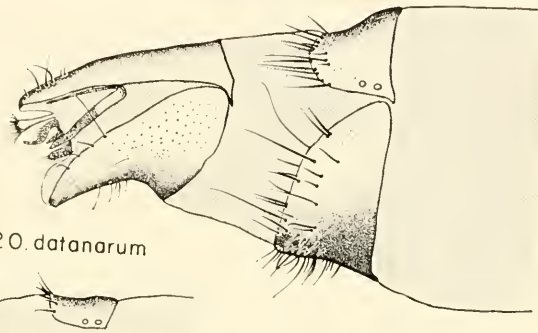
FIGURES 19-24

FIGURES 19-24.—Right lateral views of postabdomens of females of *Lespesia*. 19. *aletiae*; 20. *datanarum*; 21. *archippivora*; 22. *callosamiae*; 23. *ciliata*; 24. *cuculliae*.

FIGURES 19-24

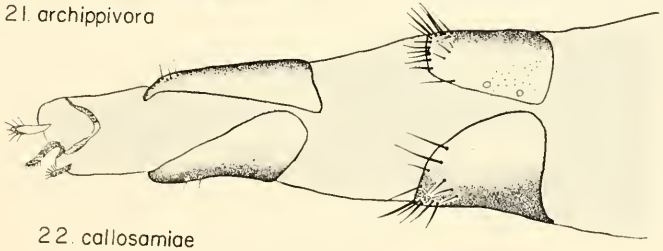


19. aletiae

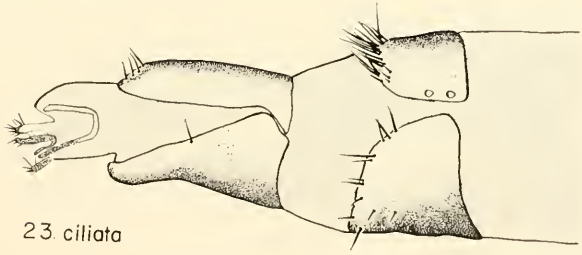


20. datanarum

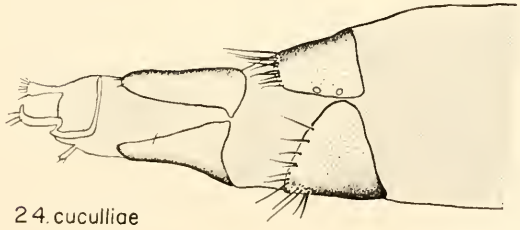
21. archippivora



22. callosamiae



23. ciliata



24. cucullíae

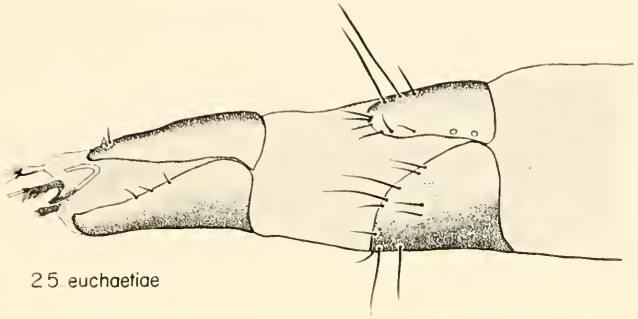
1 mm.
scale: 19-24

FIGURES 25-31

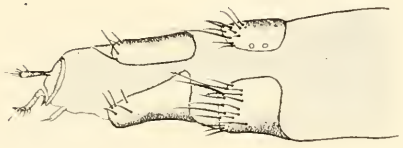
Figures 25-27.—Right lateral views of postabdomens of females of *Lespesia*. 25. *euchaetiae*; 26. *rileyi*; 27. *sabroskyi*.

Figures 28-31.—Dorsal views of postabdomens of females of *Lespesia*. 28. *aletiae*; 29. *dataiiarum*; 30. *ciliata*; 31. *euchaetiae*.

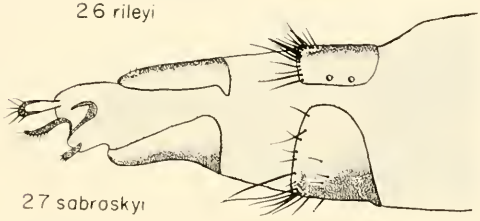
FIGURES 25-31



25 euchaetiae

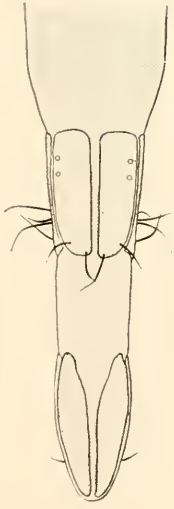


26 rileyi

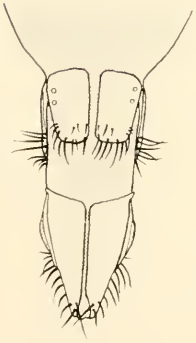


27 sabroskyi

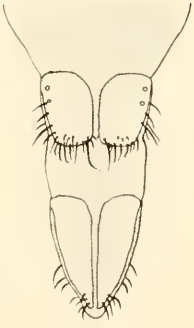
1 mm
scale 25-27



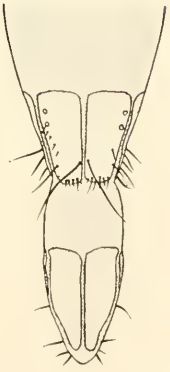
28 aletiae



29 datanarum



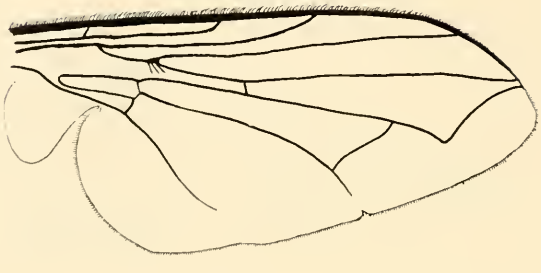
30 ciliata

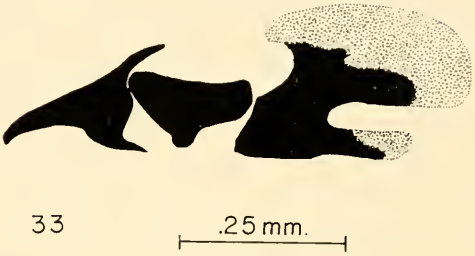


31 euchaetiae

1 mm
scale 28-31

FIGURES 32-34





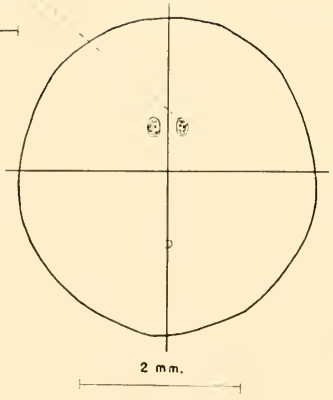


FIGURE 32.—Right wing of male of *Lespesia frenchii.*

FIGURE 33.—Left lateral view of cephalopharyngeal skeleton of third instar larva of *Lespesia frenchii.*

FIGURE 34.—Puparium of *Lespesia euchaetiae.* 34A. Posterior view of puparium showing the posterior spiracles located above the horizontal axis; 34B. Posterior spiracles of puparium.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

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The Lizards of Thailand

BY

EDWARD H. TAYLOR

ABSTRACT: The entire known lizard fauna of Thailand is treated, based for the most part on collections made in Thailand in 1957, 1958, 1960, 1961, by the author and now in the zoological collection of Chulalongkorn University, Bangkok, Thailand.

More than one hundred of the 116 species and subspecies described are illustrated by photographs in black and white.

The following new species are described:

Peropus angusticaudatus

Cnemaspis kumpoli.

A few forms are reported for the first time as occurring in Thailand.

THE LIZARD FAUNA OF THAILAND

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INTRODUCTION

The work involved in preparing this review of the herpetology of Thailand was undertaken at the specific request of Dr. Supachai Vanijuvadhana, Professor and Head, Department of Biology, and Secretary General of Chulalongkorn University, Bangkok, Thailand, who has himself long been interested in Thai faunas. Through the kind offices of Dr. Supachai, a Fulbright Grant was made available to me for the period, September, 1957, to June, 1958; and again from July, 1959, to September, 1960. In 1961 I again returned to the Far East and spent a number of months in Thailand and surrounding countries. Thus altogether nearly two and a third years were spent in the country, of which about one year and four months' time was spent in exploring and collecting either in Thailand or along boundaries of neighboring countries.

While no collector alone can hope to sample adequately the herpetological faunas of a country as large as Thailand * in so short a time, nevertheless, several thousand specimens were made available for study. These together with a study of collections in a number of European and American museums has served for the survey.

The plan of this work, as well as that on the serpents of Thailand and the turtles of Thailand (also ready) is largely that of the first volume on the Amphibia of Thailand† published in 1962. A great deal of field data and ecological observations has been omitted from the manuscript to allow for adequate illustrations. While the value of this field work is certainly not underestimated, it is recognized that this type of work can be done with greater ease and deliberation by Thai students when adequate means are available for identification of their materials.

I am most especially indebted to Dr. Supachai Vanijuvadhana who

* 225,148 square miles and extending from 6° to 21° N lat.; and from 97° to 106° E long.

† Univ. Kansas Science Bull., vol. 43, 1962, pp. 265-599. figs. 1-106.

initiated the work, and in every way possible was untiring with his help, and maintained prompt concern for my needs. He has my appreciation and gratitude.

ACKNOWLEDGEMENTS

In preparing this work numerous institutions and numerous individuals associated with them have assisted me greatly by providing space, equipment for work, and specimens for study. I am indeed under obligation to the following: Mr. J. C. Battersby, British Museum of Natural History; Dr. L. D. Brongersma, Director, and Dr. M. Boeseman of the Riksmuseum van Natuurlijke Historie, Leiden; Dr. Doris Cochran, U. S. National Museum; Dr. Josef Eiselt, Naturhistorisches Museum, Wien; Miss Alice G. C. Grandison, British Museum of Natural History; Dr. Robert Mertens and Dr. Konrad Klemmer, Senckenbergian Museum Frankfurt am Main; Dr. J. Guibè, Muséum d'Histoire Naturelle de Paris; Dr. Lothar Forcart, Museum of Natural History, Basel; Dr. Giuseppe Scortecci, Director, Institute of Biology, University of Genova; Mr. Hellenius, Curator of Herpetology, Zoologisch Museum, Amsterdam; Dr. Enrico Tortonese, Director, Museo Civico di Genova; Dr. Heinz Wermuth, Berlin Museum; Dr. Gaston-François de Witte, Musée Royal d'Histoire Naturelle de Belgique; Dr. Ernest Williams, Agassiz Museum, Cambridge.

Friends in Thailand who have been especially helpful are: Prof. Dr. and Mrs. (Dr.) Georg Heuser, Bangkok; M. L. Pootipong Nupartpat Varavudhi, Bangkok; Oliver Gordon Young and Mr. Harold Young, Chiang Mai; Dr. Boonsong Lekagul, Bangkok; Nai Prayoon Kananuracks, Na Pradoo, Pattani; Mr. and Mrs. Lynn Noah, Songkhla; Dr. Vichian, Pattani; Mr. Mann Lilipan and Mr. Vatana Lilipan, Nakhon Si Thammarat; M. R. Chakratong Tongyai, Bangkok; Prof. Kloom Vajarobala, Bangkok; Mr. and Mrs. Josef Meyer, Siracha, Chon Buri; Dr. and Mrs. Norman Meinkoth, Bangkok; Mr. Donald H. Rochlen, Bangkok; Nai C. D. Suwanarata, Na Bon, Nakhon Si Thammarat; Dr. T. D. Stahlie, Ermelo, Holland; Dr. H. A. Fehlman, Bangkok; Mr. Lim Boo-Liat, Kuala Lumpur, Malaya, and Mr. Kumpol Isarankura, Bangkok.

Friends in Malaya: Dr. John Hendrickson, Kuala Lumpur, University of Malaya, Lord Medway, University of Malaya, Kuala Lumpur, Malaya; and Mr. Eric Alfred, Raffles Museum, Singapore.

To all these I offer my sincerest gratitude.

THE LIZARD FAUNA OF THAILAND

The reptilian group Sauria, comprises all of the animals commonly called lizards and while most of them can be placed in this reptilian group by casual observations, there are many kinds that have lost arms, and legs, as well as the girdles for supporting these, and have become burrowing animals now having more the appearance of serpents than of lizards.

Even the lizards with their usual accouterments of limbs, scales, sense organs, etc., present considerable variety of shapes and sizes. Most of the differences in body-shape and character are interpreted as adaptations to environments. While most of these lizards are terrestrial in habit, many have become arboreal; some are glissant forms, gliding through the air; some have become largely aquatic, and as pointed out, some are subterranean.

Very often an examination of a lizard from an unknown locality will disclose by body-form its type of habitat. Thus the character of the toes and feet often show whether the animal is a good climber; an examination of the digital lamellae, whether they can cross ceilings, while a compressed body and long tail suggest that they are arboreal forest dwellers.

Locomotion: Locomotion among lizards is indeed varied. Those with arms and legs are able to move rapidly over the earth, or they may climb trees with ease. However some of the lizards with four limbs have developed the ability to move in bipedal fashion. This is true of certain Iguanids, some being capable of moving so rapidly that, with the use of their long tails, they are capable of running on the surface of a stream or pond of water and if not crossing it completely may move for a considerable distance upon its surface. One Agamid of Thailand, the "Yaă," *Leiolepis belliana,* when running at maximum speed often moves bipedally, but I have not seen the species attempt to cross water in this fashion.

Probably the development of the organs permitting the animal to glide through the air is the most striking adaptation for arboreal locomotion. In the Agamid dracos the ribs push out from the sides of the body carrying a fold of skin. The ribs can be moved and the skin-fold covering them can be spread out or folded back along the sides of the body. Presuming they wish to move from one tree to another, they loosen their hold on the tree and the moment they start to fall the wing is spread and the animal glides to the desired

goal. It can change its direction, avoid branches, and trees, and alight seemingly with all movement under control.

The loss of arms and legs requires the use of body muscles for locomotion, and the lizard in this condition moves much in the fashion of a snake or worm. Even some species whose limbs have become very short fold them closely along the sides of the body and move in a serpentine fashion.

Sex and reproduction: The usual expectation in any population is practically an equal number of males and females. For the most part this is the case. However in *Hemidactylus garnotii* males are rarely found throughout its range * and the same is true of *Lepidodactylus lugubris* and *L. divergens.*

All eggs are fertilized internally, the male being equipped with two separate intromittent organs which lie at the base of the tail posterior to the anus and are protruded through the cloacal opening. After fertilization the eggs may have a shell placed on them and they may be laid; or they may be retained in the uterus without a shell until the eggs are ready to hatch, the young then are born alive.

The egg coverings of most lizards are of a flexible leathery material which permits egress and ingress of water through the surface. Eggs of this kind are buried beneath the surface of the earth, presumably to prevent dessication. However, many of the gekkoes lay eggs with shells containing calcium, which makes the egg brittle. In such cases the eggs are placed in nooks and crannies or they are plastered together against a surface such as a rock, or the underside of leaves, or on a tree-trunk. Seemingly there is no water loss or gain. Most of the species hide the eggs in dark places; however, *Ptychozoon* may place the eggs on a smooth-barked tree where the egg is exposed to light and wind until it hatches. It appears that the female chooses a spot where the sun does not shine directly against them.

If the eggs are buried, the young when they hatch must burrow to the surface and escape. Young gekkoes may hatch in precarious places but the adaptation of their hands and feet is such that the lamellae adhere to the surface and the young usually emerge safely even from the underside of a leaf in a high tree.

The eggs vary much in size and shape. Some may be typically egg-shaped, rounded at one end and oval at the other while still

* One possible exception to this is *Hemidactylus garnotii* and *Lepidodactylus lugubris* on the island of Tinian. Dr. Fred R. Cagle studied the lizards there, collected many and sexed them all. No disproportion in the number of sexes is expressed and presumably not noticed. Unless one questions the identification of these lizards as reported by Dr. Cagle, one is forced to conclude that the genetic mechanism responsible for large female populations is not operable on Tinian.

others are spindle-shaped with a narrow point on each end of the egg; others somewhat elongate, rounded rather than oval at each end. Some of the Agamids of the genus *Draco* may have a small "shelf" pinched at one end of the egg. In burying the eggs, Agamids of the genus *Calotes* usually choose a rather solid area (such as a well-trampled elephant path) and dig with their hands a cuplike cavity into which the eggs are laid. The hole is refilled with earth and tamped by spreading the arms somewhat and using the head as a pile-driver! The head may strike the earth as many as a hundred times, leaving the surface above the eggs quite firm. The Ceylonese genus *Lyriocephalus* has developed a globular protuberance on the end of the snout in adults. I do not know whether this is used in pounding loose earth after egg-laying or not.

Glands: The characteristic glands of lizards are numerous. A large number of species have special glands in the scales of the head and these glands may likewise be distributed over most of the body. Dr. Giuseppe Scortecci, Instituto di Zoologia, University of Genoa has made a splendid study of these organs in the Agamidae.* A large number of genera in the families Gekkonidae, Agamidae, Lacertidae, Varanidae and Dibamidae have small organs, usually called preanal and/or femoral pores. These appear in the males and in some genera and species may also exist in the females, where they are usually smaller and often non-functional. However, the presence of these in the female is the rarer condition. In the Gekkonidae the pore-scales are usually in the same proportions and numbers but even this is not invariable. Just how these pores function is still a matter of conjecture. Some genera are such that males of certain species have femoral pores while other species lack them in both sexes. One remarkable fact seems to be that all endemic members of the family Gekkonidae in the Western Hemisphere lack the true femoral or preanal pores. In the family Eublepharidae they are present; while in the Sphaerodactylidae there is another type of organ (escutcheon scales) that occupy the same general area as the preanal and femoral pores do and one presumes they subserve the same function.

The preanal pores differ considerably in number but the usual arrangement is a continuous row on the underside of the femur meeting in the preanal region; or the femoral series may be separated from the preanal series. In some Australian and New Zealand forms there may be many series of pores and they may total more than a hundred.

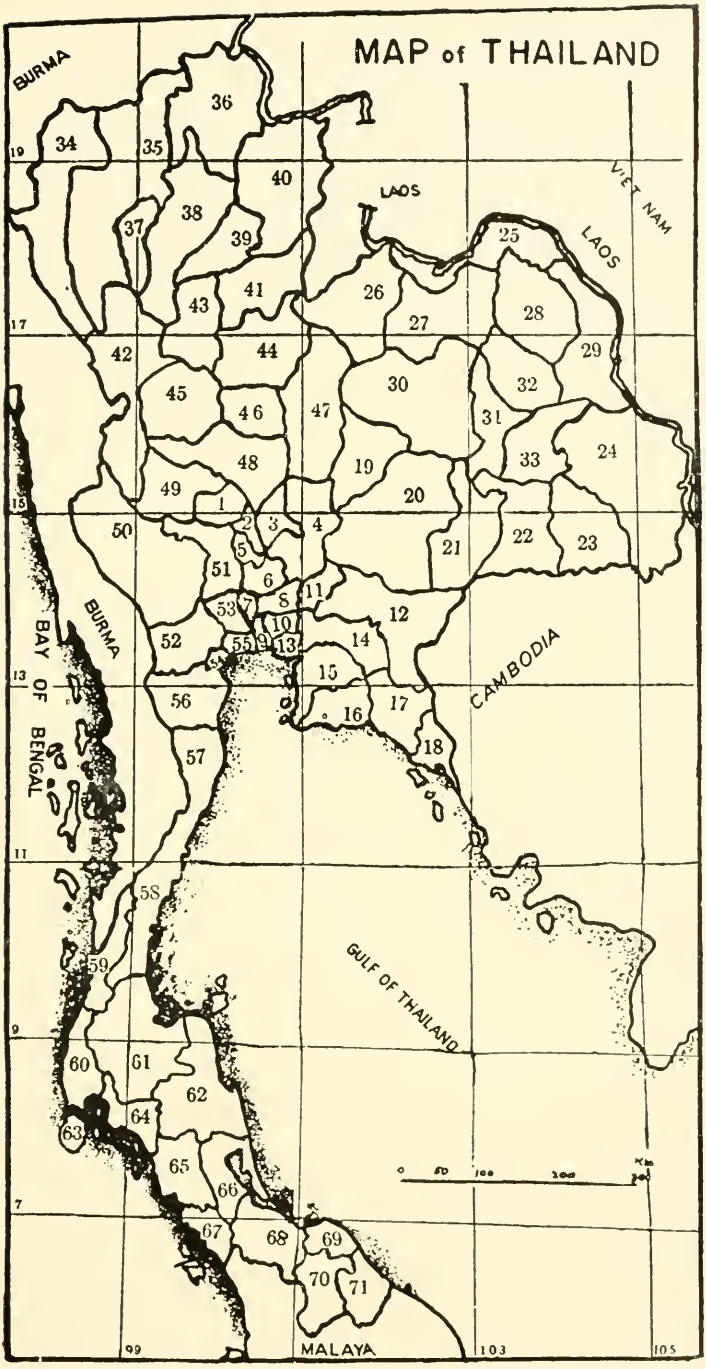
* Mem. Soc., Ital. Sci. Nat. (Mus. Civ. di Storia Nat. Milano), vol. 10, fasc. 3., 1941.

LIST OF THAI PROVINCES

(Corrected spellings as used by the U. S. Army Gazetteer, 1944)

1. Chainat
2. Sing Buri
3. Lop Buri
4. Sara Buri
5. Ang Thong
6. Ayutthaya
7. Nonthaburi
8. Pathum Thani
9. Thon Buri
10. Phra Nakhon (Bangkok)
11. Nakhon Nayok
12. Prachin Buri
13. Samut Prakan
14. Chachoengsao
15. Chon Buri
16. Rayong
17. Chanthaburi
18. Trat
19. Chaiyaphum
20. Nakhon Ratchasima (Khorat)
21. Buriram
22. Surin
23. Khu Khan (Sisaket)
24. Ubon
25. Nong Khai
26. Loei
27. Udon Thani
28. Sakon Nakhon
29. Nakhon Phanom
30. Khon Kaen
31. Maha Sarakham
32. Kalasin
33. Roi Et
34. Mae Hong Son
35. Chiang Mai
36. Chiang Rai
37. Lamphun
38. Lampang
39. Phrae
40. Nan
41. Uttaradit
42. Tak
43. Sukhothai
44. Phitsanulok
45. Kamphaeng Phet
46. Phichit
47. Phetchabun
48. Nakhon Sawan
49. Uthai Thani
50. Kanchanaburi
51. Suphan Buri
52. Rat Buri
53. Nakhon Pathom
54. Samut Songkhram
55. Samut Sakhon
56. Phet Buri
57. Prachuap Khiri Khan
58. Chumphon
59. Ranong
60. Phangnga
61. Surat Thani
62. Nakhon Si Thammarat
63. Phuket
64. Krabi
65. Trang
66. Phatthalung
67. Satun
68. Songkhla
69. Pattani
70. Yala
71. Narathiwat

As for the spelling of Thai names, I am using the scheme of transliteration from the Thai alphabet adopted by the Thai Government nearly two decades ago, and likewise used in the U. S. Army Gazetteer of 1944. This often is at variance with spellings encountered in European or older American maps, or in other reports. An effort should be made to stabilize the system of transliteration.



Map 1.—Outline Map of Thailand, showing provinces (changwats). The numbers have no significance of their own.

In certain *Cnemaspis* the pores are so minute that one may need a lens to be certain of their presence. This small size may account for reports of the absence of pores in males of certain species of this genus. While the preanal and femoral pores are absent from the Scincidae, I have recently noted a series of postanal pores in certain members of the genus *Tropidophorus*.

Poisons: Among oriental lizards not a single species is capable of transmitting a specific poison by biting and not one is known to be poisonous. The dracos have a pair of small caninelike teeth in both jaws and larger ones have sufficient jaw strength to penetrate the skin. The large gecko or Tokay is very likely to bite when being caught or held. Once when the jaws are clamped down on a finger or on a bit of skin the teeth may not penetrate the skin, but if the bitten part is withdrawn suddenly usually an area of the skin is scratched or injured leaving an unpleasant but not necessarily a serious wound.

Voice: The lizard species of the family Gekkonidae have a voice mechanism and are capable of making a sound of their own volition. The "*tokay*" has the loudest call and this is usually easily recognized and well known. The smaller domestic geckoes called *chinchook* also have a voice, and these sounds are easily recognized. It is not known whether the single representative of the Eublepharidae has a voice or not.

Occasionally other kinds of lizards are reported as having a call but this most probably is due to hearing a sound and seeing an animal at the same time without the certainty that the sound is produced by the animal. I have had a report that the flying dracos produce loud sounds but this is doubtless a case of uncertainty as to the source of a sound heard. These species certainly have no voices.

METHODS

The general plan of this work follows that of the Amphibians of Thailand, published in 1962. Since that work was completed the new International Rules of Nomenclature and Procedure has been published. In consequence in this work on the Saurians I have attempted to follow the proposed regulations such as the use of the colon after authors names in the listing of literature. The recording of type-localities where these are known for original names and synonyms.

The spelling of Thai geographic names has caused no small difficulty since the available maps show great diversity. This is because the Thai alphabet has many more characters available than the English and there is no consensus as to the proper spelling of the Thai word and certainly none for the proper method of transliteration into English. In reporting the distribution of the various species I have listed for the most part only the *Changwat* or province rather than publish the catalogue of all the specimens collected. This of course is a measure for economy. In the spelling of the province names I have used the spelling of the U. S. Army Gazetteer of 1944. Among the other geographic names, while I have attempted to follow the same criterion, many are not so transliterated. There are perhaps some inconsistencies in the spellings. One other difficulty has been the fact that the geographical divisions have themselves been changed. Thus formerly much of the present southern part of peninsular Thailand consisted of Pattani which was further divided into several smaller states. These have now ceased to exist and Pattani now consists of three Changwats, Pattani, Narathiwat and Yala.

The specimens in the collection largely brought together by me form the basis for this study, and all numbers unless otherwise designated belong to that collection. In a number of cases other specimens have been photographed or described and abbreviations have been used. These abbreviations are as follows:

AMNH	American Museum of Natural History, New York.
B.L.	Private collection of Dr. Boonsong Lekagul, Bangkok.
B.M.	British Museum (Natural History), London.
C.U.	Chulalongkorn University more recent acquisitions, Bangkok.
EHT-HMS	Edward H. Taylor-Hobart M. Smith Collection, Lawrence, Kansas.
NHMW	Museum, Vienna.
KUMNH	Kansas University Collection, Lawrence, Kansas.
M.S.	Malcolm Smith, private collection (chiefly in the British Museum).
N.P.K.	Private collection of Nai Prayoon Kananuracks, Na Pradoo Pattani.
USNM	United States National Museum, Washington, D. C.

TAXONOMIC CONSIDERATION OF ORDER SAURIA

KEY TO THE FAMILIES OF SAURIA

1. Diminutive, wormlike lizards with a single large plate covering most of snout; eyes covered; arms absent; legs present as two small flaps at sides of vent in males only; two or four preanal pores, scales uniform, cycloid, imbricate ..... *Dibamidae*
   Lizards of various sizes, usually not with a single scale covering most of snout, or, if so, no sexual dimorphism in limbs 2
2. Very large lizards, one to three meters in length, covered with small tuberculate juxtaposed scales, each surrounded by a row of minute tubercles; tongue long, slender, deeply bifid, retractile into a sheath; always pentadactyl; an elongate tail; head with numerous small scales above ..... *Varanidae*
   Smaller lizards, under one meter in length; tongue not as described above; without rows of minute tubercles surrounding scales; limbs may or may not be pentadactyl 3
3. Scales covering top and sides of head not enlarged or symmetrical ... 4
   Scales covering top and sides of head enlarged, symmetrical, or if with small scales and tubercles, the teeth acrodont (Agamidae) 5
4. Vertebrae procoelian; parietal bone single; eye with thick movable connivent eyelids; claws retractile ..... *Eublepharidae*
   Vertebrae amphicoelian; parietal bone divided ..... *Gekkonidae*
5. Teeth acrodont, varying in shape and not replaced; tongue thick; femoral pores absent in Thai species (except in the genera *Leiolepis* and *Physignathus*) ..... *Agamidae*
6. Inguinal or femoral pores; back covered with large rhomboidal keeled shields forming longitudinal series; tail extremely long (Thai form) ..... *Lacertidae*
   No femoral, preanal, or inguinal pores; body covered with cycloid imbricating scales above and below; tail usually about equal to snout-vent length, rarely twice as long; osteoderms often present; rarely postanal pores or glands ..... *Scincidae*

FAMILY EUBLEPHARIDAE Boulenger

True eyelids present, without "spectacle"; pupil vertical; vertebrae procoelous; parietal bones united; digits straight, slender, without lamellae claws usually partly concealed or retractile; postanal sacs and bones present; body often compressed.

This family is represented sparingly in both Eastern and Western Hemispheres. Of the two Asiatic genera, *Eublepharis* and *Aeluroscalabotes*, only the latter has been taken within the confines of Thailand, this is in the southern part. However, the presence of two species in India and another in Hainan and one in the Riu Kius suggests that another species may occur in the northern part of Thailand if the generic distribution is not discontinuous.

Three species of *Aeluroscalabotes* have been described. These are strange-looking lizards with a head twice as wide as the neck

and wider than the body, which is more or less compressed. The tail is relatively short. The claws are retractile into sheaths, and true moveable eyelids are present.

Of the genus *Eublepharis* one species is found in northwestern India, and one on the island Hainan. One presumes that the distribution is discontinuous.

Aeluroscalabotes Boulenger

Aelurosaurus (*non* Owen) Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 73 (*felinus* type of genus).

Aeluroscalabotes Boulenger, *ibid.*, vol. 3, 1887, p. 482.

Diagnosis: Digits short, sub-cylindrical at base, compressed, in distal phalanges, which are raised and furnished with a claw that is retractile between the three plates forming a compressed terminal sheath; transverse thickened lamellae at base of underside of digits; distal scales small, numerous; body with small nearly uniform juxtaposed flat scales; upper and lower eyelids well developed; pupil vertical. Males with preanal pores.

Only a single species is recognized in Thailand and Malaya. Two others, however, have been described.

Aeluroscalabotes felinus (Günther)

Fig. 1

Pentadactylus felinus Günther, Reptiles of British India, 1864, p. 117, pl. 12, fig. F (type-locality, Singapore).

Aelurosaurus felinus: Boulenger, Catalogue of the lizards in the British Museum, Ed. 2, vol. 1, 1885, p. 73, pl. 3, fig. 8.

Aeluroscalabotes felinus: Boulenger, Catalogue of the lizards in the British Museum, Ed. 2, vol. 3, 1887, p. 482; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore including the adjacent islands; Reptilia and Batrachia, 1912, pp. 39-40; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 6, no. 3, July 1924, p. 317 ("Patani").

Diagnosis: (see generic description).

Description of species (from EHT-HMS No. 3168; Selangor, Malaya, 1961): Head strongly triangular, more than double width of neck. Body and neck strongly compressed; tail shorter than body, also somewhat compressed; rostral large, more than twice as wide as high, bordered behind by two large supralabials, two nasals and three other enlarged scales; behind these scales a group of twelve large scales arranged in two irregular rows; nostril surrounded by one nasal, which seems to surround nostril completely; bordering this rim is a small "supranasal," the first labial, and four or five small scales; eye length (7 mm.) equal or slightly less than its distance to nostril; a slight depression behind nostril; a depression in frontal

FIG. 1.—*Aeluroscalabotes felinus* Günther, EHT-HMS, No. 3168, Selangor, Malaya. Actual length, 186 mm.

and interorbital areas; auricular opening largely below level of corner of mouth, its distance from eye, nine millimeters, its diameter, 1.3 millimeters; eye with a vertical pupil; upper and lower eyelids rather well developed; supralabials, 12-13, last small; mental with a labial border nearly equal to that of rostral, followed by two somewhat irregular chinshields; twelve infralabials, last large; a row of much-enlarged scales on each side of lower jaw bordering infralabials, anteriorly touching chinshields.

Scales on dorsal part of head small, nearly uniform, juxtaposed, biscuit-shaped, somewhat elevated, their surface granular or corrugated seen under a lens; scales on side of snout distinctly smaller, granular, those on body slightly larger than on head, those on venter slightly larger than on dorsum; an angular series of 25 enlarged scales of which median ten are perforated or with small pits; caudal scales nearly smooth, a little larger than body scales, forming perfectly straight transverse rows around tail.

Limbs slender, tip of each digit provided with an enlarged sheath composed of a small dorsal and two large lateral scales into which claw is retracted; fingers short, subcylindrical at base with thickened transverse lamellae, the series on various fingers cross palm; distal part of fingers with five to seven rows of fine scales instead of lamellae; the lamellae on toes continuous across sole; distally toes have rows of from three to five scales; when arm and leg are laid along body they overlap about twelve millimeters.

Color: Dorsal and lateral parts of head and body uniform brown with two lines of dim tan spots beginning on occiput, continuing on dorsum to base of tail; lower surfaces of head and venter cream, dotted with brown; upper lip, chin, and throat cream; tail brown, on dorsal surface of a somewhat darker shade and with four cream

Measurements in mm. of *Aeluroscalabotes felinus*

NUMBER	M. 140	No. 3168	M. 141
Snout to vemt	106	112	76
Tail length	80	74	?
Total length	186	186	?
Width of head	20	19	13
Length of head	25.5	25.5	19
Tip of snout to arm	39	42	32
Axilla to groin	55	58	36.5
Arm	34	32	23
Leg	41.5	42.5	30

All from near Kuala Lumpur, Selangor, Malaya.

spots, with dark brown borders on their basal third; on subcaudal region several cream spots usually associated with dark-brown spots or flecks; distal part of tail uniform brown.

Variation: The sides of the head are often considerably darker than the top. Occasionally the color is quite different. Boulenger (1912) states: "Brown above, with two dorsal series of more or less distinct lighter, dark-edged roundish spots; sometimes scattered white dots on the sides of the body." There are 12 small preanal pores on No. 141 and one or two adjoining scales have pits; the outer scales of the series stand nearly erect tending to overlap the next outer scale.

The posterior edge of the pupil is smooth, the anterior crenellated. Two strong lateral tubercles are present on sides of base of tail, the area about them being cream. There is no web or only the faintest trace of a web between digits.

Distribution: A single specimen of this species has been taken in Thailand. It was captured at "Benang Star," Yala province (formerly in Pattani province).

Outside of Thailand the species has been reported from Singapore (the type locality) and the Larut Hills, in Perak, Malaya. It has also been reported from Borneo.

Remarks: Concerning the two other species described in this genus, *A. dorsalis* and *A. longicauda*, Dr. Malcolm Smith (1930) states: "I strongly doubt if *A. dorsalis* Peters, 1872, and *A. longicauda* Anderson, 1924, should be regarded as distinct; the characters on which they are based seem to be varietal, rather than specific." This matter should be reinvestigated since Dr. Smith has left much room for doubt.

The specimen described was captured at night on a plant growing out of the water of a small stream. It was not especially active. In the laboratory at Kuala Lumpur it was kept in a small cage in which was placed a dish of water. The animal, a gravid female, entered the water and remained partially submerged for several days until it was preserved.

FAMILY GEKKONIDAE GRAY

The proper limits of the Family Gekkonidae have been in doubt for some time. G. A. Boulenger in the British Museum Catalogues recognized three families of gekkolike lizards: the Eublepharidae, Uroplatidae, and the Gekkonidae proper. Certain recent taxonomists have found and defined a fourth group, the Sphaerodactylidae,

seemingly worthy of family recognition, a group confined to the Western Hemisphere.

One sees in these four families, relationships that suggest that they are members of the same superfamily. It is believed that the interest of taxonomy is best served by recognizing these groups as family groups. Only two of these are Asiatic, the Gekkonidae, and the Eublepharidae, and each likewise has representatives in the Western Hemisphere.

The best known representatives of the Gekkonidae are the small, domestic species living in houses and other buildings as well as in original forest. The Thai name applied to several small species is "*chinchook*," and to a large domestic species of the gecko, *to-kay*. Certain of the species that live on the ground or trees are seldom seen or if seen, are not recognized as different from the domestic forms.

There are nine genera of the Gekkonidae known in Thailand. These are *Cyrtodactylus* (formerly *Gymnodactylus*), *Cnemaspis*, *Hemidactylus*, *Peropus*, *Platyurus*, *Hemiphyllodactylus*, *Gekko*, *Phyllodactylus*, and *Ptychozoon*. These will be treated later.

General Characteristics of the Gekkonidae

The Thai species of this family may usually be recognized by having the dorsal and lateral part of the body covered with soft granules or scales often intermixed with larger tubercles. In *Phyllodactylus* these enlarged tubercles, usually trihedral, almost cover the dorsum. The ventral surface of the body usually is covered by cycloid scales. Males of many of the species have small "glandular" pores in scales situated somewhat anterior to the vent (preanal pores) and others may have a longer or shorter series along the underside of the thigh (femoral pores); these may be continuous with the preanal series. These pores are usually present in males and rarely tiny pores may be discovered in the females of certain species (*Cyrtodactylus*) but seemingly they are not functional. The numbers of pores are variable, reduced to one or two on each side (*Cnemaspis*) or there may be sixty or eighty forming a large cluster as in *Rhacodactylus*. The purpose served by femoral and preanal pores has not been learned.

Many of the genera have specialized structures on the digits that enable them to run or crawl about a ceiling or wall as easily as on a floor. These consist of widened overlapping lamellae which have very fine papillate processes, the purpose being to cause adhesion

to a smooth surface; these are evident only in arboreal species (or those secondarily adapted to human dwellings or rocks). The claws are not lost (or at most only one from a hand or foot) and these are of service when the animal has to crawl over a surface that is too rough or uneven for the adhesive pads to be serviceable. These lamellae may be arranged in a single row, may be in double rows, or may form rosettes near the tip of the digit. *Cnemaspis* and *Cyrtodactylus* are exceptions that cannot climb on nor cross smooth ceilings. The Thai species of *Phyllodactylus* living on the ground have a pair of widened lamellae near the tips of the digits, but I have not observed that these lizards are as adept at climbing as species of New World *Phyllodactylus* are capable of doing. Adhesive lamellae are absent in the genera *Cnemaspis* and *Cyrtodactylus*.* However, several such species are capable of climbing in tree trunks, some seemingly typically arboreal in habit, often feeding under bark of dead trees.

In the Gekkonidae, just posterior to the anus there are two small sacs opening to the outside. Partly within each sac in the males and lying below the skin is a small curved postanal bone. The sacs but no bones are present in females. These curious structures are present also in the family Eublepharidae, but absent in the family Sphaerodactylidae. There is no secretion from the sacs and their function is not clearly known.

A single Oriental genus (*Pristurus, fide* M. Smith) occurring in India is said to lack the postanal sacs and bones. I have not examined a representative of this genus, but at present it is usually placed in the family Gekkonidae.

Tails of species of this family are fragile and easily lost or broken. When broken they wiggle and twist serving often to attract the attention of a predator from the animal itself. The tail, when lost, except in rare cases, is grown again. This reproduced part contains cartilage but no bones and the tail rarely has the same external characteristics as the original tail, but it will usually reach the length of the original. Usually, if not always, the subcaudal scales are much wider than those of the original tail, and the dorsal and lateral tubercles and scales themselves may be different. One can, with care, invariably distinguish the reproduced tail from the original.

Members of the Family Gekkonidae and the Eublepharidae are the only lizards with a voice mechanism; most other lizards are silent. Some others may make a slight hissing sound but this is rarely

* Formerly regarded as *Gymnodactylus*.

the case; if the air is forcibly extruded from the lungs, a slight squeak may sometimes be produced.

KEY TO THAI GENERA OF THE GEKKONIDAE

1. Digits slender lacking adhesive lamellae 2
   Digits at least partly widened with at least some adhesive lamellae 3
2. Pupil round ..... *Cnemaspis*
   Pupil a vertical slit; or when further closed appears as a vertical series of small openings ..... *Cyrtodactylus*
3. A single terminal pair of widened lamellae between which the claw is retractile ..... *Phyllodactylus*
   More than a single pair of adhesive lamellae 4
4. Tail strongly lobulate laterally, sometimes widened at tip; a lateral winglike expansion on each side of body and head ... *Ptychozoon*
   Tail not lobulate; a lateral fringe of skin present on side of body or not 5
5. A fringe of skin from axilla to groin; tail with a denticulate fringe, *Platyurus*
   No skin-fringe along side of body 6
6. Subdigital lamellae undivided; terminal joints of outer digits united with expanded part of digit; inner digit clawless ..... *Gekko*
   Terminal joints of digits not united with the widened lamellae; subdigital lamellae divided 7
7. Inner digit well developed 8
   Inner digit vestigial, without free terminal joint, clawless or with a minute claw; subdigital lamellae divided or single, *Hemiphyllodactylus*
8. Inner digit well developed, without free terminal joint, the claw minute, often concealed ..... *Peropus*
   Inner digit well developed, with a free, clawed terminal joint, *Hemidactylus*

Genus CYRTODACTYLUS Gray

Cyrtodactylus Gray, Phil. Mag., vol. 2, 1827, p. 55 (type of the genus *Cyrtodactylus pulchellus* Gray).

Diagnosis: All digits slender with claws surrounded by two scales, lower very large, notched below claw; upper scale small; distal phalanges usually compressed making an agle with proximal part of digit, which is flattened, with short series of enlarged flat plates or lamellae, contiguous or imbricate; subcaudal scales enlarged, either paired, or median series transversely widened; preanal or femoral pores (sometimes both) present. (One specimen of *oldhami* reported in which only one pore is present, another with none [*fide* Malcolm Smith]); scales of females have "impressions" but are not or but rarely perforated; median postmentals form a common suture behind mental; generally three or more scalerows on sides of digits; pupil vertical tending to form tiny openings when not dilated (*Gekko*-type pupil).

The genus *Cyrtodactylus* has been revived by Garth Underwood for species occurring outside the Western Hemisphere formerly placed in the genus *Gymnodactylus*. This latter name is restricted to South American species, a group, none of which has preanal or femoral pores. Most if not all of the species known in the old world have pores (see *oldhami*). The structure of the "eyelids" is different in *Gymnodactylus* and *Cyrtodactylus*.

There are, within the boundaries of Thailand, at least nine forms of this genus. At the tin mine (Tonka Harbour Tin Dredging Co., Rompibun) I obtained a specimen of what may have been another species, presumably undescribed. It was golden yellow in general color with some brown markings, but it escaped from a plastic bag, the only container available at that time, by the simple expedient of tearing a slit in it with a claw. No others were encountered. It was found ensconced under moss-grown, rotting bark, on a large stump.

The specimens are seen in the daytime only when they have been routed from hiding places; none has been seen in Thailand moving about of its free will in the daytime. Several species have been found roving at night and captured, while others were seen that escaped capture. I presume that in general they are nocturnal. The character of the lamellae under the toes does not permit them to move over a smooth ceiling as many geckoes do. Their strong claws, however, enable them to climb well on tree trunks or in caves. Certain species are more terrestrial than arboreal and occupy places on or under fallen logs or fallen bark. Two eggs are laid, but I have not discovered where they are placed.

Taylor and Elbel (Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, p. 1041) include *consobrinoides* Annandale in their list of species occurring in the Thailand fauna. This is an error, resulting from a misidentification, no specimens having been taken. It has, however, been taken at Tavoy, Tenasserim, Burma, about thirty miles from the Thai border, and very likely occurs in peninsular Thailand in the Bilauk Taung border range.

KEY TO SPECIES OF CYRTODACTYLUS IN THAILAND

1. Foot partially webbed; tail with lateral denticulations; nine preanal pores on either side; brown with W-shaped dorsal marks in young which may disappear in adults ..... *brevipalmatus*
   No web present on hand or foot 2
2. Preanal and femoral pores present 3
   Only preanal pores present (rarely absent in *oldhami*) 4

3. Preanal pores 12-13, forming a A-shaped series enclosing a groove; femoral pores four to six on each side, widely separated from preanal series; no dark, light-edged band from eye around occipital region ..... *marmoratus*

   Preanal pores eight, in two parallel rows lying in a deep groove but contiguous, at right angles, with a long series of femoral pores; a curved or angular, light-edged band from eye around back of occiput; body with transverse, light-edged, dark bands .... *pulchellus*

4. No median continuous series of transversely widened subcaudal scales 5

   A median series of transversely widened subcaudals in a continuous series except on basal 24 millimeters of tail 6

5. The median series usually paired or rarely with occasionally fused scales; male with preanal pores in an angular series of scales sometimes not strongly developed; a series of somewhat specialized femoral scales, without pores; four somewhat W-shaped marks of brown or black on dorsum ..... *angularis*

   No dark band passing from eye to eye behind occiput; body with four or three longitudinal stripes originating behind eye.. *quadrivirgatus*

6. Male with one or two preanal pores on each side (rarely absent); brown or dark brown with whitish elongate or rounded spots tending to form longitudinal rows on dorsum; curved dark light-edged band from eye around occiput ..... *oldhami*

   Male with five or more preanal pores 7

7. Male with seven or eight preanal pores; paired median series of dark spots and a lateral series of transversely widened dark spots (often tending to fuse) all in a reticulum of cream-white; head with a white reticulum enclosing dark spots ..... *peguensis peguensis*

   Body marked with transverse bands (sometimes broken) 8

8. Body banded with seven transverse dark-edged bands, separated by narrow gray interspaces; top of head with a light reticulum enclosing darker spots; eight or nine preanal pores, *peguensis zebraicus*

   Body gray or gray-brown marked with four distinct bands of dark brown or blackish brown each edged with yellow or cream; a light-edged brown band from eye around occiput; top of head uniform brownish; preanal pores eight to ten; venter with 40-50 rows of scales at middle of body ..... *intermedius*

Cyrtodactylus brevipalmatus (M. Smith)

FIGS. 2, 2a

Gymnodactylus brevipalmatus M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 6, 1923, p. 48, pl. 5, fig. 1 (type-locality, Khao Luang, Nakhon Si Thammarat Mts., Peninsular Siam); Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 55 ("Hills near Raheng, Ban Pa Che, northern Siam.").

Diagnosis: A medium-small species (greatest length known, 72 mm. snout to vent); ear-opening one sixth of eye diameter; about 44 scales across venter between the ventrolateral folds; folds bearing

enlarged tubercular scales; nine very large preanal pores, six-seven femoral pores; no pubic groove; toes with webs at base. Brown above, with or without indistinct spots.

Description of species (data from type-description): Head moderately depressed, snout little longer than orbit; ear-opening small,

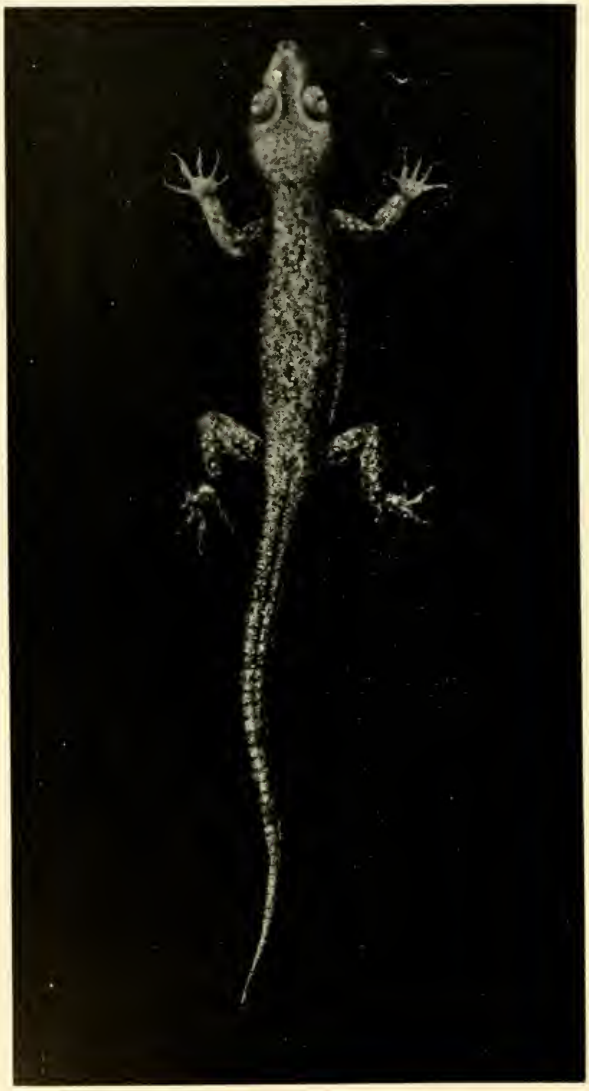


FIG. 2. — *Cyrtodactylus brevipalmatus* M. Smith. Fig. after M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 6 1923, pl. 5, fig. 1. Khao Luang, Nakhon Si Thammarat, Mts., Thailand.

oval, one sixth of diameter of eye; head covered with small granules, largest over snout, those on occiput intermixed with small tubercles; rostral quadrangular, broader than high, bordering nostril first labial, two supranasals, and two small internasals; an entrant suture from top edge, bifurcating, its branches continuing somewhat, forming an angle greater than a right angle; supralabials, 12-13, first bordering nostril; infralabials, 10-11; mental large, subtriangular; first pair of chinshields large in contact with each other followed by two pairs of smaller scales, these widely separated. Throat and chin covered with small flat granular scales; dorsum with fine granules

FIG. 2a.—*Cyrtodactylus brevipalmatus* (M. Smith). From M. Smith, Journ. Nat. Hist. Soc. Siam. vol. 6, 1923, pl. 5, fig. 1 (*part.*)

interspersed with enlarged rounded keeled tubercles; indistinct ventrolateral folds with enlarged scales, separated on venter by about 44 rows of small cycloid scales. A series of nine much enlarged preanal pores forming wide angle; six and seven femoral pores separated by an interval from preanal series; enlarged scales preceding and following pore-scales; no pubic groove.

Tail cylindrical, tapering, covered with small scales and regularly disposed rows of keeled tubercles above, with irregularly disposed enlarged scales below. Limbs moderate, digits long, toes webbed at base and strongly compressed distally. Basal part of digits with six or seven broad imbricate transverse plates below.

Color: Brown above with obscure darker mottlings; much paler below.

Measurements in mm. (Type, No. 6367, and a topotypic paratype No. 6366): Snout-vent length, 64, 72; tail, 77, ?; arm, 19, 23; leg, 30, 35.

Remarks: The types were collected on Khao Luang at an altitude of 750 meters in the Nakhon Si Thammarat mountains in the province of this name, by H. M. Pendlebury, Esq., in March, 1922. This species has not been obtained since. The second specimen, No. 6366, is a female; there are 35 scales across the venter. The ventrolateral fold is distinct. The specimen is brown above with small irregularly disposed black spots. The venter and throat are also faintly spotted.

The presence of a small web between the toes will separate this form from other Thai members of the genus. The arrangements of the femoral and preanal pores differ from the other local species. Both type and paratype were found on trees hiding under dead bark.

Cyrtodactylus marmoratus (Kuhl)

Phyllurus marmoratus Kuhl, in Fitzinger, Neue klassification der Reptilien nach ihrem natürliehen Verwandtschaften, 1826, p. 47 (type locality, Java).

Cyrtodactylus marmoratus: (*part.*) Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 173.

Gonyodactylus marmoratus: Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9, Synopsis, 1831, p. 51; Girard, U. S. exploring expedition, vol. 20, herpetology, 1858, p. 304.

Gymnodactylus marmoratus: Duméril and Bibron, Erpétologie générale . . . vol. 3, 1836, pp. 426-428, plate 34, figs. 1, 1a; Schlegel, Abbildungen neuer oder unvollständig bekannter Amphibien . . . 1837, p. 8, 1837, pl. 2; Steindachner, Reise der oesterreichischen Fregatte Novara um die Erde in den Jahren, 1857-1858-1859, Wien, 1867, p. 17; Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, pp. 44-45; Flower, Proc. Zool. Soc. London, 1899, p. 626; Laidlaw, Proc. Zool. Soc. London, vol. 1, 1901, p. 304; Boulenger, Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 148; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 35-36; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 3, p. 153 (Sai Yoke district, Kanchanaburi province); *ibid.*, vol. 2, 1916, p. 151 ("Bangnara and Patani"); *ibid.*, June, 1916, p. 61; Journ. Federated Malay States Mus., vol. 10, 1922, p. 268; Kopstein, Treubia, Buitenzorg, vol. 11, 1930, p. 304; Bull. Raffles Mus., no. 10, 1935, p. 62; *ibid.*, no. 14, 1938, pp. 137-138; ? Gibson-Hill, Bull. Raffles Mus., Singapore, no. 18, 1947, pp. 81-86 (Christmas Island); Brongersma, Versl. gewone Vergad. Akad. Amsterdam, vol. 62, no. 10, 1953, pp. 172-175.

Diagnosis: Ear-opening one third of diameter of eye; median cleft in rostral; slight ventrolateral fold bearing row of tubercles from axilla to groin. Males with 12-13 preanal and 4-6 femoral pores; tail with uniform flat scales without enlarged tubercles; light brown above with chestnut-brown spots, sometimes confluent into cross-bands on back; tail with brown annuli.

Description of species (from Boulenger, 1885): Head rather large, depressed, oviform, snout longer than distance between ear-opening and eye; forehead with depression; ear-opening suboval, oblique, not quite one third diameter of eye. Body and limbs rather elongate. Digits strong, slightly depressed at base, strongly compressed distally; basal phalanx with well-developed transverse plates inferiorly. Head granular, with very small tubercles on occipital and temporal regions, granules on snout rather enlarged; rostral subquadrangular, not twice as broad as high, with median suture entering from above; rostral borders nostril, first labials, supranasals, and internasal scales; ten to twelve supralabials; nine to ten infralabials; mental triangular; two or three pairs of chinshields, median largest, in contact behind point of mental; throat minutely granulate; body and limbs covered above with small granules intermixed with small roundish, feebly keeled, subtrihedral tubercles; a more- or less-defined series of tubercles from axilla to groin tending to form a ventrolateral fold delimiting venter; ventral scales small, cycloid, imbricate.

Males with twelve to thirteen preanal pores in a A-shaped series enclosing a groove; a row of four to six femoral pores widely separated from preanal pores. Tail cylindrical, tapering, covered with uniform small flat scales above, with a few scattered tubercles.

Color: Light brown above with chestnut brown spots, which are sometimes confluent into cross-bands on back; tail, when intact, with dark-brown annuli; chestnut-brown streak on side of head, passing through eye; lower surfaces brownish.

Measurements in mm.: Snout to vent, 76; tail, 72; total length, 148; width of head, 15; length of head, 21; arm, 26; leg, 34.

Distribution: The species has been reported in Thailand from "Bangnara, Patani" [= Narathiwat, Narathiwat province] and Bukit Besar, Pattani. There are a number of records for the species in Malaya. In the Indonesian region it has been reported from Sumatra, Java, and Celebes.

Remarks: There is seemingly an unrecognized species of this genus occurring in Sumatra and Java. It bears a resemblance to *marmoratus* but the pubic groove of the male contains one very large plate perforated by a single huge pore. The scales on each side of the groove lack pores, and the extended series as it reaches the femora may have small pores, very tiny perforations, or merely pits, or the scales may be smooth. Some specimens seen have the head spotted somewhat after the manner of *peguensis*.

There is a specimen in the British Museum (BM 63.12.11.173, RR 1946.9.7.44) which may be a specimen of a species identified as *Gymnodactylus agamensis* Bleeker in the Vienna Museum. It has a large pore in a single plate in a pubic groove. I have not found the original description of this species since the name (if the species name appearing on certain museum specimens was actually published) has been overlooked by subsequent workers. Spots on the body of the specimen tend to form more or less distinct transverse rows. The proximal part of the tail has tubercles on each segment, the distal part being strongly banded in dark brown and cream. There are about 18 rows of fine scales between the pore-scales and the vent.

A specimen of "*marmoratus*" from Bukit Besar, Pattani, Thailand, is a female and the characters of the pores are wanting, however, between the pores-scales and the vent there are seven rows of enlarged preanal scales. The rostral is bordered behind by five scales.

A form also occurs in Java, having a median plate bearing a large pore, and the femoral pores are a little better developed than in Sumatra specimens examined.

A review of these forms must be undertaken when material is available.

Cyrtodactylus pulchellus Gray

FIG. 3

Cyrtodactylus pulchellus Gray, Zool. Journ., vol. 3, 1828, p. 224 (type-locality, Singapore); Illustrations of Indian Zoology, vol. 2, 1834, pl. 74; Gray, Synopsis reptilium, in Griffiths' Cuvier's Animal kingdom, vol. 9, 1831, p. 51; Catalogue of the lizards in the British Museum, 1845, p. 173.

Gonyodactylus pulchellum: Wagler, Natürliches System der Amphibien, 1830, p. 144.

Gymnodactylus pulchellus: Duméril and Bibron, Erpétologie Générale . . ., vol. 3, 1836, pp. 423-425, pl. 33, fig. 7, 7a, 7b (?"Cette belle espèce de Gymnodactyle est originaire du Bengale"); Günther, Reptiles of British India, 1864, p. 113; Cantor, Catalogue of Malay Reptiles, 1847, p. 25, reprint from Journ. Asiat. Soc. Bengal, vol. 16; Stoliczka, Journ. Asiat. Soc. Bengal, vol. 42, 1873, p. 118; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 46-47; The fauna of British India, Ceylon and Burma; Reptilia and Batrachia, 1890, pp. 69-70; Flower, Proc. Zool. Soc. London, 1896, p. 863; *ibid.*, 1899, pp. 626-627 (Penang Hill 2000-2400; Larut Hills, 3400-4400 ft.); Fasciculi Malayenses Zool., vol. 1, 1903, p. 148; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 36-37; Annandale, Rec. Indian Mus., vol. 9, 1913, p. 325; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, p. 150 ("Khao Wang Hip, Nakon Sritamarat," Thailand); Mertens, Blätt. Aquar.-Ter. Jahr. 40, Heft No. 6, 1929, pp. 101-102, pl. 16, fig. 2; M. Smith, Bull. Raffles Mus., Singapore, no. 3, April 1930, p. 13.

Diagnosis: A large species reaching 115 mm. snout to vent; tail 144 mm.; body and tail banded dorsally and laterally with dark and

FIG. 3.—*Cyrtodactylus pulchellus* Gray. No. 35747, Khao Chong, Trang, Thailand. Actual length, 229 mm.

light bands. Top of head uniform gray-tan; preanal pores in two closely approximated longitudinal series in a deep groove, forming a right angle and continuous with series of from 15 to 20 femoral pores; subcaudals much enlarged, transversely widened, three fourths or more of the tail width.

Description of species (from No. 35747, Khao Chong Forest Station, Trang province, Thailand): Rostral large, (3 x 5.2 mm.), nearly erect, bordering nostril, first supralabial, two supranasals and an internasal; a median suture enters scale above, runs down for nearly one millimeter then bifurcates, the branches continuing for .8 millimeter; nostril surrounded by first supralabial, two postnasals, a supranasal, and rostral; neither of the postnasals seem to be fused to valvelike flap within nostrils; internasal nearly as large as supranasal; about 43 scales in a row across snout at back level of second supralabial; about 68 scales in a row across snout between seventh supralabials; about 70 scales across head between palpebral scales at middle of eyelid; length of snout (12 mm.) greater than distance between ear-opening and orbit (10 mm.); area posterior to nostril depressed; depressed area beginning on occiput continues forward between orbits widening and terminating in a sharp angle on snout; granules on snout variable in size, largest immediately following supranasal and internasal; next largest bordering supralabial and in the region anterior to upper part of eye; median and anterior occipital scales small, granular, intermixed with conical tubercles smaller than those on posterior part, which in turn are smaller than dorsal body tubercles; supralabials, 13-14, diminishing in size posteriorly, their surfaces rough, tubercular, and followed to mouth-angle by 12 undifferentiated scales; infralabials, 12-12, eighth on left side (ninth on right) split longitudinally; following infralabials to mouth-angle are eight to nine undifferentiated small scales; mental narrowed and pointed posteriorly, its labial border equal to that of rostral; pair of chinshields posterior to mental forming common suture for about one fourth of their length, about 2.5 times as long as wide; second pair of chinshields half as long as first pair, and separated by first pair; the two pairs bordered behind by four small scales; two or three rows of sublabials, somewhat enlarged; granules in a row on chin and throat, from chinshields to line drawn between front of shoulders, approximately 103; from front of shoulder to vent approximately 82; scales on dorsum, small, pavementlike, uniform, intermixed with about 24 irregular rows of trihedral or pyramidal (rarely conical) tubercles somewhat variable in size; scales

on tail in transverse rows, nine to eleven on each segment, last two rows with six or four enlarged tubercles, or more posteriorly with only two tubercles; hemipenes causing pair of strong postanal swellings; subcaudals greatly enlarged, three fourths to four fifths of width of tail, two belonging to each segment; approximately 79 subcaudals, terminal 28 millimeters of tail regenerated; regenerated scales not much widened, and not resembling those preceding; on each side of subcaudal row a series of somewhat widened scales larger than adjoining caudal scales. Dorsal part of arms, except elbows, legs, except knees, with numerous enlarged tubercles, those on legs largest; pair of distinct ventrolateral folds separated from each other by about 35 scalerows; those in median area largest, mostly cycloid, imbricating; eight preanal pores in deep longitudinal groove in preanal region forming two longitudinal rows of four and continuous at right angles with a long series of 14-15 femoral pores, which occupy scales of an enlarged series on underside of thigh.

Digits with flat imbricating somewhat widened lamellae on basal part; seven or eight on longest finger, eleven on longest toe; the distal joints crooked; penultimate joints arising from following phalanx, curving forward to tip with 13 or 14 compressed lamellae under longest finger and fourteen under longest toe; claw surrounded by two scales, lower widened on both sides and narrowed below, upper scale small; no web present.

Ear-opening small, vertical diameter about two millimeters with a slight fold above and below partly hiding opening, about one fourth of diameter of orbit (8.7 mm.).

Color in life: Head nearly uniform tan without spots; dark brown band begins behind eye and passes around occiput, widening on dorsal part of neck, bordered anteriorly and posteriorly by narrow line of cream bearing numerous cream-colored tubercles; on body four cream-edged transverse bands (third bifurcating on right side); tail with 7 + bands of dark brown to blackish, not passing across ventral surface of tail.

Chin and venter cream-white, subcaudal region for most of its length lavender to violet; labials gray-white; sides of snout a little darker than dorsal part.

Measurements in mm.: Snout to vent, 102; tail, tip regenerated, 127; total length, 229; snout to arm-insertion, 40.5; axilla to groin, 45; width of head, 23.6; length of head, 32; arm, 34; leg, 50.5.

Remarks: A single specimen was captured May 18, 1957, at Khao

Chong Forest Station from the trunk of a forest tree, near a small stream, late at night. A second specimen was seen in the nearby resthouse were I stayed, running along the floor to a small opening and escaping under the house floor; on a second visit another specimen was found in a crevice in a tree.

Variation: Flower (1899) regarded the species as living chiefly on rocks and in caves in Malaya but it is obvious that it is not confined to such habitats. He reports a male specimen having a snout-to-vent measurement of 115 mm.; tail, 144 mm. There were 36 femoropreanal pores altogether in the specimen.

Distribution: In Thailand the species is known from Phattalung, Trang, and Nakhon Si Thammarat provinces.

The species was described as early as 1828 by J. E. Gray, whose type-specimens came from Singapore. It is known from numerous localities in Malaya and up to elevations of 3400-4400 ft. in the Larut Hills of Perak. It has also been taken in Bengal; and Tenasserim, in Burma.

Cyrtodactylus angularis (M. Smith)

FIG. 4

Gymnodactylus peguensis angularis M. Smith, Proc. Zool. Soc., London, 1921, no. 19, p. 427, text fig. 1A (on p. 28), (type-locality Dong Paya Fai Mountains, [not Dong Rek as originally stated, in error]).

Gymnodactylus angularis: M. Smith, Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2; Sauria; Feb. 7, 1935, p. 52 (Pak Jong, Hin Lap, and Lat Bua Kao, Khorat [= Nakhon Ratchasima] province).

Diagnosis: Grayish above; light brown, black-edged band beginning on snout, passes through eye, and from eye around occiput where it becomes much widened; band bordered anteriorly with cream. Body with three W-shaped or butterfly-shaped marks separated by gray bands each with numerous black flecks; tail banded. Six preanal pores in broadly angular series; 40 scalerows between ventrolateral folds; two pairs of chinshields; no median preanal groove; a few widened subcaudal scales may be present.

Description of species (from No. 33377, Pasadet, Sara Buri, province): Rostral about twice as wide as high, subrectangular, standing nearly erect, bordering first labial, nostril, supranasals, and internasal; suture enters from above and extends down distance of about one-half millimeter where it bifurcates, the branches continuing four millimeters farther; nostril surrounded by supranasal, rostral, first supralabial, and two postnasals, the lower continuous with valvelike flap inside nostril; depressed area behind nostril; depression on

FIG. 4.—*Cyrtodactylus angularis* M. Smith. Left figure No. 33377, Pasadet, Sara Buri; actual length, 174.5 mm. Right figure No. 33376, 2 kilometers east of Muk Lek Road Camp, Nakhon Ratchasima province, Thailand. Actual length, 178 mm.

interorbital region continuous with one on frontal area; about 33 scales in row across snout just behind level of second supralabials; about 47 scales across snout between seventh labials; scales on snout mostly flat, pavementlike, those in front of inner edge of eyelid somewhat conical; scales on frontal and interorbital areas growing smaller posteriorly; granules on occiput small, only one fourth to one fifth size of lateral scales on snout, and intermixed with enlarged, usually conical, tubercles; about 56 granules between edges of eyelids across middle of interorbital region; supralabials, 15-14, diminishing in size posteriorly, and followed to mouth-angle by nine scales, not differentiated; infralabials, 10-11, followed by a few undifferentiated scales; labial border of mental little smaller than rostral border; mental subtriangular, followed by median pair of chinshields in contact for at least half their length, nearly twice as long as wide; second pair of chinshields separated by first pair, their length little more than half of first pair; third pair indicated by small scale on one side only; one or two rows of slightly enlarged sublabials; about 87 granular scales in row between first chinshields and line across front of shoulders; scales very small on chin and throat, larger, imbricating on breast; about 103 scales from level of shoulders to vent, variable in size, mostly cycloid, imbricating; an angular series of enlarged scales in preanal region, three on each side bearing preanal pores; this series continuous with a series of twelve enlarged femoral scales without pores; behind preanal porescales four enlarged rows of scales followed by nine rows of small scales reducing in size posteriorly; slight ventrolateral fold on which there is a broken series of enlarged conical tubercles; approximately 48 ventral scalerows between folds, median ones somewhat cycloid, imbricate, outer series much smaller and granular.

About 35 tail segments, basal 15 with about eight transverse rows of small flat tubercles above and on sides, with last two or three interrupted by much enlarged series of six conical or trihedral tubercles; towards posterior part of tail these tubercles reduce from six to four and then to two. Terminal segments without enlarged scales; segments can be discerned with difficulty; median subcaudals enlarged, usually two paired scales and large single scale below each segment; occasionally enlarged scale split longitudinally; postanal openings distinct, large; postanal region strongly swollen in male with three lateral tubercles on each side.

Distal part of digits narrowed, forming crook near middle of digit; fourth finger and toe with six flat scales on basal part, and

12-13 scales on distal part of digit; no webbing present; when leg is adpressed toes reach axilla. Arms and legs with numerous distinct tubercles.

Color in life: Above, head gray-brown with several small darker-edged spots; body gray becoming whitish on latter half of tail. A brown irregular dark-edged stripe from nostril through eye, passes around occiput much widened dorsally, bordered by a light-edged stripe around occiput; three large paired spots or double blotches somewhat W-shaped or butterfly-shaped on back; twelve or thirteen dark bands on tail growing darker posteriorly; bands on body and tail separated by broader gray bands, more or less flecked with dark brown or black, each with a dark-edged ocellus on each side; lip cream with brown spots; chin and venter cream; light bands in subcaudal region flecked with brown or black; dark bands completely encircling tail.

Table of measurements of *Cyrtodactylus angularis*

NUMBER	33376 ♀	33378 ♀	33377 ♂
Snout to vent	82.5	92	80
Tail	92	regen.	95.2
Total length	174.5	.....	175.2
Snout to arm insertion	32	36	32.2
Axilla to groin	36.5	44	37
Length of head	24	25.5	23.5
Width of head	18	20	17.6
Arm	31.2	32	32
Leg	39	41	38
Pores	3–3	3–3	3–3
Ventral scalerows between fold	45	42	40

Variation: The females have small femoral pores or at least pits or scars on the scales. No. 33376 has all except three of the enlarged subcaudal scales divided; the basal segments have only two series of paired scales usually the anterior pair smallest; more posteriorly there may be two pairs of much smaller scales and one pair of larger scales. This specimen also came from Pasadet.

No. 33378 was taken about two kilometers east of Muak Lek Road Camp (on Friendship Highway) in Nakhon Ratchasima province near its boundary with Sara Buri. All three specimens came from under limestone rocks.

The largest specimen has two large eggs in the body. The regenerated tail of this specimen is about 40 mm. long but is black, the

scales not in rows, lacking tubercles. The gray dorsal bands are darker and the lateral spots are not or scarcely ocellate. The dark flecks on the gray bands usually have linear arrangements.

Besides these specimens Malcolm Smith had three specimens in his type series, one each from Lat Bua Kao, Pak Jong, and Hin Lap, Nakhon Ratchasima province, Thailand.

Distribution: The species is known from only the provinces of Sara Buri and Nakhon Ratchasima.

Cyrtodactylus quadrivirgatus Taylor

FIG. 5

Cyrtodactylus quadrivirgatus Taylor, Univ. Kansas, Sci. Bull., vol. 43, 1962, pp. 210-212, fig. 1 (type-locality Khao Chong, Forest Experiment Station, Trang province, Thailand).

Diagnosis: Small scales under tail, lacking a median series of enlarged plates; four preanal pores in males; in females four very small pores or four scales with deep depressions; no continuous black band extending from eye to eye across occiput; four dark lines from head to tail separated by lighter lines, or the two median dark stripes broken, forming united spots on dorsum. Tail with transverse black bands separated by lighter bands.

Description of type: A rather small species; rostral not twice as wide as high, its upper edge with a V-shaped notch cutting scale half in two, the area of notch being filled with three internasal scales; rostral bordered by these three scales, first supralabial and nostril; nostril bordered by rostral, first labial, a large and a small supranasal, and three small postnasals; 56 scales across snout between fifth supralabials; about 64 small granular scales between median edges of eyelids; eye diameter less than snout length; ten smooth supralabials, posterior ones small, followed by eight or ten small granular scales reaching back to angle of mouth; ten infralabials, last three small, followed by seven very small scales to mouth-angle; mental triangular with a labial border equal to that of rostral; a pair of chinshields separated for more than half their length by mental; second pair of chinshields separated by five scales, scarcely differentiated; ear diagonally elongate, tympanum deeply sunk; a slight depression on occiput more or less connected with a depression on snout.

Scales on occipital region very small with a few scattered rounded tubercles; dorsum with somewhat larger granular scales intermixed with minute scales and with large conical or pyramidal tubercles

FIG. 5.—*Cyrtodactylus quadrivirgatus* Taylor. Type. Khao Chong Forest Experiment Station, Trang province, Thailand; actual length, 144 mm.

forming about 24 irregular rows; a bare trace of a ventrolateral fold, separated from its fellow by about 40 scalerows, the outer rows small, median ones considerably larger; group of four preanal pores continuous with a series of 17 enlarged femoral scales. Tail above dimly segmented; dorsal scales smaller than ventral ones; no median widened series of scales on undersurface of tail but there may be four or five series subequal in size, a little larger than dorsal caudal scales; no caudal tubercles; tail slender, tapering to a fine point. Legs reach to elbow of adpressed arm; toes subequal, six or seven lamellae under basal part of fourth toe; all digits clawed.

Color in life: Above gray on body; head uniform blackish on top; a distinct black band begins behind eye extending back on sides of body to base of tail, bordered above by a wide gray stripe and below by a narrow one; two other lines begin behind eye and run back to form an angular union on nape; they then separate and continue to tail, where they are rejoined; median gray line interrupted in two places by connecting lines between the two median dark stripes; a very indistinct darker line low on sides; chin and venter uniformly whitish with a peppering of black. Tail banded with black and gray, the basal gray bands including some black; underside of tail blackish with white flecks; gray bands surrounding tail only on distal part; some indistinct lighter flecks on labials; arms and legs with spots or bands of black above, whitish below.

Measurements in mm. (of type and No. 388, a paratype): Snout to vent, 67, 39; tail, length, 77, 22 (broken); snout to arm, 32, 16; axilla to groin, 34, 19; width of head, 13, 8; length of head, 18, 13; arm, 21, 13; leg, 26, 17.

Remarks: The color pattern of the young male topotypic paratype is quite similar to the type. There is, however, some indication of lighter and darker areas on the head. The distal part of the tail has been lost. In the Malayan specimens the two median stripes are broken sometimes forming a series of spots.

The relationship of this species may be with *Cyrtodactylus oldhami*, however, the absence of the enlarged transverse subcaudal series of scales, and the absence of the curving band about occiput from eye to eye suggests a different relationship. *Oldhami* may lack pores. Absence of femoral pores would seem to preclude close relationship with *marmoratus*.

The type specimens were found at an elevation of about 400 meters on Khao Chong, under a decaying log. A specimen of *Cnemaspis siamensis* was taken in the immediate vicinity.

Cyrtodactylus oldhami (Theobald)

FIG. 6

Gymnodactylus oldhami Theobald, Descriptive catalogue of the reptiles of British India, 1876, p. 81 (type-locality unknown; originally said to be South Canara,* India): Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 38; Fauna of British India including Ceylon and Burma, 1890, p. 67; Annandale, Journ. Asiat. Soc. Bengal (N. S.) vol. 1, 1905, p. 83; Rec. Ind. Mus., vol. 9, 1913, p. 320, pl. 17, fig. 2. "The type is a male and one scale of this series (the enlarged scales in the preanal region) bears a distinct pore. In the other males there are 4 preanal pores arranged in two pairs." Mintao, Tavoy district, Tenasserim; Tavoy); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 150 (Maprit and Klong Bang Lai, 60 km. N. Isthmus of Kra); Journ. Nat. Hist. Soc. Siam, vol. 2, June, 1916, p. 51 "Patiyu, Peninsular Siam"; Fauna British India, including Ceylon and Burma; Reptilia and Amphibia; vol. 2, Sauria, Feb. 7, 1935, p. 50, pl. 1, fig. C. "Patiyu district, and Nakon Sritamarat Mts."

Diagnosis: Snout as long as distance between eye and ear-opening; diameter of ear-opening about one half of diameter of orbit. About thirty rows of trihedral tubercles on back and sides; 34-38 ventral scales between lateral folds; paired series of large tubercles on tail; a median subcaudal scale series, transversely widened except at base. Male with 1-4 (total) preanal pores; no femoral pores in enlarged series of femoral scales; no pubic groove; top of head uniform brown; body with elongated or rounded spots arranged in four longitudinal lines. Snout to vent 65 mm.

Description of species from EHT.-HMS., M. 246 (M. Smith 4300): Rostral large, wider (4 mm.) than high (2 mm.) with a median groove from its upper edge halfway to mouth; small supranasal separated from its fellow by two small scales; nostril surrounded by rostral, supranasal, first labial and one other small scale (the upper part of the labial scale excludes several small scales from bordering nostril); twelve supralabials followed by ten or eleven small scales to mouth-angle; 46-50 small scales across eyelids and interorbital region (at middle of eyelid); about 47 scales across snout between fifth supralabials; occipital scales minute, with scattered tubercles; orbit shorter than snout; mental with labial border equal to that of rostral; one pair of enlarged chinshields, forming a mutual suture for half their length, touching infralabials; ten or eleven infralabials; two or three larger scales border labials behind chinshields; auricular opening moderate. A shallow frontal concavity. Digits of hands and feet slender, clawed; distal portion of digit forming an angle with proximal joint; fingers with two or three widened platelike lamellae with an enlarged subarticular plate fol-

* Boulenger (1885) states South Canara. Annandale, *loc. cit.* states that there is no real evidence that the lizard occurs in South India. Malcolm Smith (1935) states that the type-locality is unknown.

lowing these distally; this in turn followed first by two or three divided lamellae and then by several single imbricating scales; fourth toe with six basal lamellae and the enlarged subarticular plate; claws between two plates.

Dorsal scales small, juxtaposed; tubercles intermixed with larger

FIG. 6.—*Cyrtodactylus oldhamii* (Theobald). Figure of type, from Annandale, Rec., Ind. Mus., vol. 9, 1913, pl. 17, fig. 2.

rounded, keeled or subtrihedral or pyramidal tubercles forming about twenty irregular rows on dorsum and sides; ventral scales, larger, cycloid imbricating on venter; on neck and chin, scales granular, subequal, juxtaposed; in preanal region a A-shaped series of preanal scales much larger than other ventral scales, some of which have pits; this series of scales is continuous with a femoral series of enlarged unperforated scales that extend to end of femur; this series followed behind by two other series of enlarged scales without pits. (Males with one to four preanal pores, rarely absent altogether.) Scales on legs with smaller and larger granules intermixed, and with tubercular scales on underside of forearm and tibia, the scales larger, cycloid, imbricating. Tail segments not clearly indicated except basally where three or four segments have a whorls of four or six enlarged keeled tubercles, the other scalerows consisting of small imbricate scales. There is a subcaudal series of enlarged transverse scales (occasionally divided) continuing to regenerated part of tail. They begin a short distance behind the vent (making approximately a total of 94 in specimens with a complete tail).

Color: Above gray-brown, top of head nearly uniform brown; a dark band curves from eye to eye behind occiput, bordered in front and behind by a cream-line; dorsum brown with a series of four longitudinal lines of small cream or whitish dots. Tail dark brown with dorsal cream-bars often passing under tail, many of the dorsal and especially lateral tubercles with bright cream-yellow tips; dirty whitish below.

Measurements in mm.: (EHT-HMS Nos. M. 246, and M. 247) Snout to vent, 68, 63; tail, 69 (regen.), 70 (tip regenerated): width of head, 13, 13; length of head, 21.5, 20; arm, 22, 20; leg, 32, 30.

Variation: The second specimen, No. M. 247, has two oviductal eggs.

Males may have a series of four preanal pores or they may be reduced to one. The female specimens show small pits in the scales. Trace of a small ventrolateral fold can be seen in the described specimen but not in the gravid female. There are about thirty-three scales between ventrolateral folds.

Distribution: The species has been taken in the provinces of Chumphon and Nakhon Si Thammarat, the specimens here listed being from the first province. These bear M. Smith's tags, nos. 4300 and 4299, respectively. They are from about 60 miles north of the Isthmus of Kra.

Remarks: Malcolm Smith reported three specimens from Maprit, a station on the Southern Railway, 15 km. inland from and due west of Patiyu; and from Klong Bang Lai, a camp on a stream of the same name 12 kilometers northwest of Maprit in the district of Patiyu-(Chumphon). The only male, a half grown one, has no preanal (or femoral) pores. "One scale bears a slight impression but is not perforated." He reports that the variation in pores is from 0-4.

Cyrtodactylus peguensis (Boulenger)

Gymnodactylus peguensis Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 314, pl. 7, fig. 2 (type-locality, Palon, Pegu); Laidlaw, Proc. Zool. Soc. London, 1901, p. 304; Boulenger, A vertebrate fauna of the Malay Peninsula . . . 1912, p. 36 ("Patelung and Legeh"); Annandale, Rec. Ind. Mus., vol. 7, 1912, p. 91; *ibid.*, 1913, p. 323; M. Smith, Journ. Nat. Hist Soc. Siam, vol. 2, 1916, p. 150 ("Khao Wang Hip, Nakhon Sritamarat," "80 mm. snout to vent"); Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 50-51; Proc. Zool. Soc. London, 1921, p. 427, text fig. 1a.

This species whose type-locality is Palon, Pegu District, Burma, is known from very few specimens. Annandale first reported its presence in Thailand in 1912 at Patthalung; later Malcolm Smith obtained specimens from the area about Nakhon Si Thammarat from the province of the same name. He also described a large form, 80 mm. snout to vent from the Langbian Plateau in southern Annam in 1917 which he named *peguensis irregularis*, while specimens from southern Thailand were referred to the typical *P. peguensis*. Specimens of a *Cyrtodactylus* from Central Thailand were named *peguensis angularis*. In his later work (Smith 1935), *irregularis* and *angularis* were both correctly recognized as distinct species.

Two specimens taken at Khao Chong, Forest Station, in the mountains of Trang province differ from the typical forms from Pegu some 800 miles northward. The difference is largely in the detail of the dorsal markings and the relationship of the labial to nostril and the larger ventral scales resulting in fewer ventral rows. It is not recognized as being subspecifically distinct. Numerous specimens were taken at Na Bon, Nakhon Si Thammarat.

The description of *peguensis* given by Boulenger (1912) and quoted by Annandale (1913) is taken from the type-description and not from a Malay specimen. The specimen figured by Malcolm Smith (P. Z. S. 1921) is most probably from Burma. On page 427 he states of the *forma typica:* "7-8 preanal pores; 9-11 upper and 7-9 lower labials; two series of (6-8) large round spots on the back

or with the spots confluent transversely." It may be that the specimen showing "spots confluent transversely" is the subspecies described herein as *Cyrtodactylus p. zebraicus.*

Cyrtodactylus peguensis peguensis (Boulenger)

FIG. 7

Diagnosis: Head with about 18 spots separated by a reticulum of cream; a sharply defined stripe from behind eye around occiput widening and somewhat angulate on dorsum of neck; seven or eight pairs of dark-brown or black spots, flanked laterally by a series of lateral vertical bars their upper parts brownish black, their sides blackish, their lower parts gradually becoming white and lost on venter; body spots separated by narrow reticulum of cream-white. Arms and legs somewhat barred with light and dark; the nine black rings surrounding tail, separated by white rings about half as wide as black rings, and each bearing a pair of black flecks (often other flecks may be present). No ventrolateral folds; approximately 32 scalerows across venter; seven to nine preanal pores forming a wide angle. Subcaudals (except for basal 15 mm. of tail), enlarged, transverse; the first labial enters nostril.

Description of species (from No. 35749, Khao Chong, Forest Station, Trang): Head moderately flattened, with depressed interorbital area continuous with depressed frontal area; sides of snout somewhat compressed, with slightly depressed area behind nostrils; rostral (3 mm. wide, 1.6 mm. high) bordering nostril, first infralabials, two supranasals and a small internasal; a straight median suture enters from above and extends down on scale a distance equal to half its height; nostril surrounded by rostral, two supranasals (the posterior small), first labial, and postnasal that is fused to valvelike flap within nostril; 30 scales across snout at posterior level of second labials; 41 scales between middle of fifth labials; across head, 46 scales between palpebral scales at middle of eyelids; scales on occiput smaller than elsewhere on head, intermixed with small rounded conical tubercles much smaller than those on dorsum of body; infralabials, 11-11, diminishing in size posteriorly, followed behind to mouth-angle by seven small scales; infralabials, 9-9, followed by five small scales to mouth angle; mental with labial border distinctly less than that of rostral, in contact behind with a pair of chinshields nearly three times as long as wide and in contact for more than half their length; one or two other pairs lateral to first, widely separated; two rows of somewhat enlarged sublabials; about

74 granules in a line on chin and throat between chinshields and a line in front of shoulders, the posterior scales enlarged and cycloid; approximately 72 scales from front of shoulders to vent along median line.

Scales on dorsum of body, small, subequal, intermixed with about 20 irregular rows of large conical or trihedral tubercles; arms lacking distinct tubercles; legs tubercles numerous; two or three large tubercles at side of postanal swelling; postanal pockets distinct; preanal pores in large quadrangular scales forming a broad A-shaped series of seven pores; no femoral pores or enlarged scales contiguous with pore-series; tail segmented, each segment with about seven imbricating rows, last two rows broken, by six (basally), four or two enlarged tubercles; below, on tail, scales of transverse series increase in size; on basal part of tail scales somewhat irregular, but from there on median series transversely widened, two to each segment; about 71 subcaudals, the terminal ones small and but little differentiated; digits short, basal lamellae not much widened, five or six under each digit; distal part of digit somewhat compressed; claws present on all digits, each claw surrounded by two scales; no enlarged scales at heel; ear-opening (1.5 mm.) contained in diameter of orbit (4.4 mm.) about three times.

Color in life: Above head and body with brown or blackish brown spots separated by reticulum of cream; on back seven or eight pairs, these flanked laterally by a series of lateral vertical bars, their upper parts brownish black, their sides blackish, their lower parts gradually becoming white and lost on venter; tail banded in dark brown or black; bands separated by white bands somewhat more than half as wide and bearing black flecks. Chin venter, and under limbs, whitish; venter with peppering of black pigment, visible under a lens.

Measurements in mm. (Nos. 35749, 35748): Snout to vent, 60, 67; tail, 61, 53 (regenerated); total length, 121, 120; snout to arm-insertion, 24, 28; axilla to groin, 28, 31.5; width of head, 12.8, 14; length of head, 19, 21; arm, 22, 25; leg, 27.5, 32.

Remarks: The second specimen, also a male, has a regenerated tail that is entirely gray-black with numerous darker flecks above and below. My specimens were captured from masses of plants at the base of forest trees near a stream, late in the afternoon. The specimens were exposed by tearing apart masses of plants and trash.

Distribution: Known in Thailand from Trang and Nakhon Si Thammarat provinces.

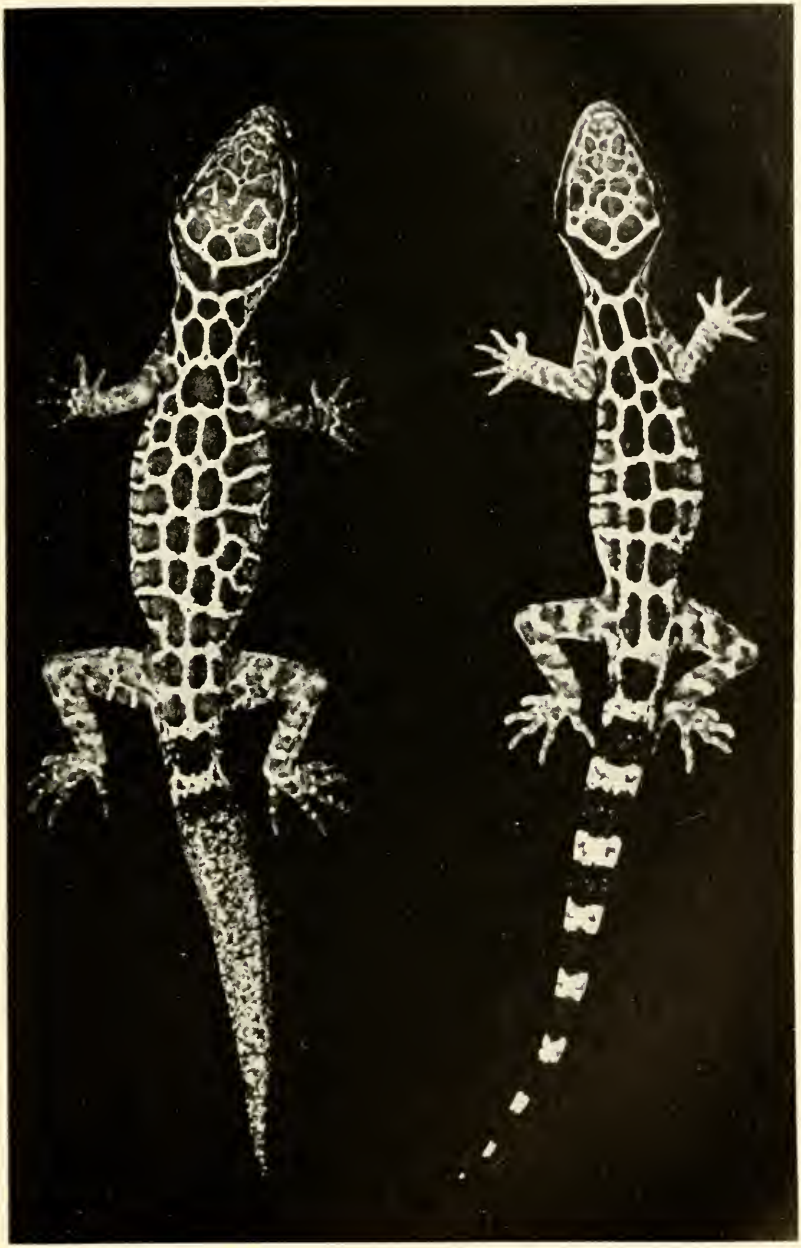


FIG. 7.—*Cyrtodactylus peguensis peguensis* (Boulenger). Left figure, No. 35748 Khao Chong, Trang province. Actual total length, 120 mm. Right figure, No. 35749 ♂, same locality, length, 121 mm.

Cyrtodactylus peguensis zebraicus Taylor

FIG. 8

Cyrtodactylus peguensis zebraicus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 213-215, fig. 2 (type-locality, Tonka Harbour Tin Dredging Co., Ronpibon, Nakhon Si Thammarat, Thailand).

Diagnosis: Head somewhat depressed, spotted above; brown bar behind eye more or less confluent with angular band bordering occiput behind; body with pair of spots on neck and eight transverse stripes wider than gray interspaces; certain of these may be discontinuous, while last, between legs, broken mesially; eight femoral pores; no ventrolateral fold.

Description of type: Head moderately depressed; length of snout a little longer (1.1 mm.) than distance between orbit and ear-opening; strongly depressed area on frontal region extending back between orbits; snout rather compressed with slight depression in front of nostril; rostral about twice as wide as high, bordering nostril, first labial, pair of supranasals, and two small internasals; nostril surrounded by first labial, rostral, two supranasals one large and one small; postnasal seemingly fused to flap within nostril.

There are 32 scales across snout between posterior ends of 2nd supralabials; across snout between anterior part of fifth labials, 49 scales; occipital region with small scales intermixed with rounded, somewhat conical tubercles, much smaller than tubercles on back; supralabials, 11-11, very small posteriorly, followed to angle of mouth by five or six small scales; nine infralabials, followed by four scales to mouth-angle; pair of chinshields, about twice as long as wide forming a common suture for about half their length; mental with labial border distinctly larger than rostral border; second pair of chinshields about half as large as first pair, widely separated by first pair; 77 granules in a row between chinshields and a line drawn from front level of shoulders; from breast to vent, 76 scales; a wide-angled series of eight preanal pores with two angular rows of larger scales between pores and vent; two large lateral postanal tubercles. Tail lost and beginning to regenerate.

Digits short, basal part scarcely widened with two or three flat imbricate scales; distal part somewhat compressed; two scales surround claw; no ventrolateral folds; about 35 scalerows across venter. Scales on sides and dorsum small, equal, interspersed with about twenty rows of enlarged trihedral tubercles. Diameter of ear-opening (1.2 mm. high) four times in diameter of orbit (5 mm.); adpressed leg does not reach axilla.

FIG. 8.—*Cyrtodactylus peguensis zebraicus* Taylor. Type. Ronpibon, Nakhon Si Thammarat, Thailand. Actual length, 58.5 mm.

Color in life: Above blue-white with transverse brown stripes with blackish edges. Head with about twenty dark spots in a blue-white reticulum; venter and chin cream-white with fine powdering of black, visible under a lens. Dark band from eye passes around occiput, angular rather than curving; lips dark spotted; regenerated tail blackish.

Measurements in mm.: Snout to vent, 58.5; snout to arm-insertion, 23; axilla to groin, 26; width of head, 12; head length, 19.4; arm, 22; leg, 28.

Remarks: This specimen was taken from a large rotting stump in the forest at Tonka Harbour Tin Mine, Ronpibon, Nakhon Si Thammarat. Its relationship is certainly with *Cyrtodactylus peguensis*, but whether a species or subspecies there may be question.

Cyrtodactylus intermedius M. Smith

FIGS. 9, 9a

Gymnodactylus intermedius M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1917, pp. 221-222 (type-locality, Khao Sebab (Mt.) near Chanthaburi, Chanthaburi province, southeastern Thailand); Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 44-45, plate 1, fig. F. (Kamchay mountains, Cambodia, Koh Chang Id. Gulf of Siam); Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1081-1082 (? Phatthalung, Thailand).

Diagnosis: Male with eight to ten preanal pores in a wide-angled series; a group of enlarged preanal scales and a series of from six to ten enlarged femoral scales; ventrolateral folds distinct, separated by from 40 to 50 scalerows on venter; ear-opening less than half diameter of eyes; subcaudal plates transversely widened; a cream-edged, dark-brown band from eye around occiput; four bands cross body; tail banded in dark and light; resembling *C. pulchellus* but lacking longitudinal median preanal groove.

Description of species (from No. 35440, topotype): Rostral not twice as wide as high, upper part bending backward with a median entrant suture from above, forming anterior border of nostril, touching first labials and three median scales, two supranasals and an internasal; first supralabial, two postnasals, supranasal and rostral complete border of nostril; three somewhat enlarged scales bordering supranasal behind; two median scales behind small median internasal; depressed areas behind nostrils; forehead somewhat concave; about 27 scales across snout between posterior level of second supralabials; approximately 49 scales across snout between seventh labials; approximately 51 granules between palpebral borders of

FIG. 9.—*Cyrtodactylus intermedius* (M. Smith). No. 35440 Khao Sebab, Chanthaburi Thailand. Actual snout-vent length, 61 mm.; total length, 93 mm.

eyelids at middle; scales on snout three or more times larger than scales on occiput or interorbital area; granules on back small with about 17-18 irregular rows of enlarged conical or trihedral tubercles; granules above eye unequal in size; ear-opening small, its diameter (1.5 mm.) about one third of the diameter of eye (4.5 mm.); eye to ear-opening (5.5 mm.) less than snout length (7 mm.); supralabials, 11-11, followed by nine small, scarcely differentiated scales; infralabials, 11-11, followed by ten or eleven small scales to mouth-angle;

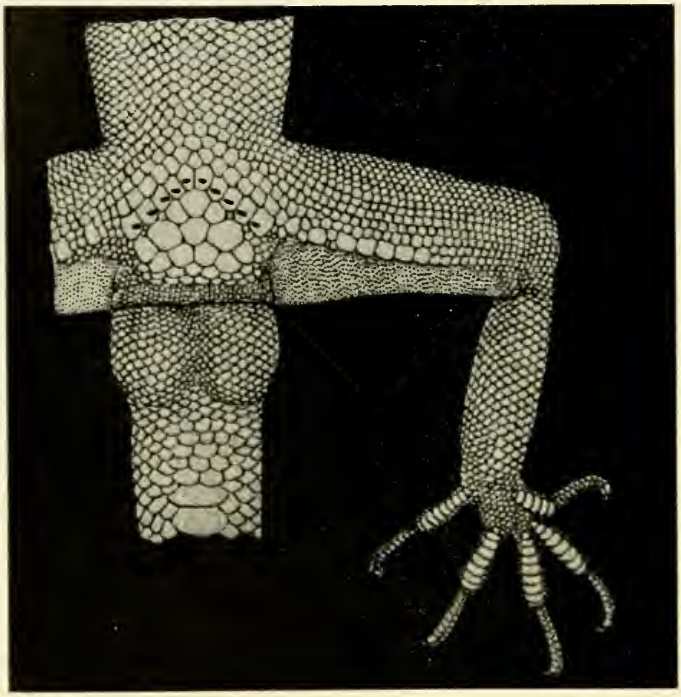


FIG. 9*a*.—*Cyrtodactylus intermedius* (M. Smith). From M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 3, 1917, pl. —, fig. 2.

mental subtriangular with a labial border equal to or slightly greater than rostral border on mouth; median pair of chinshields twice as long as wide, in contact for less than half their length; second chinshields separated, about half length of the median pair; third pair of scales less than half size of second pair; approximately 100 scales in a row from chinshields to level of shoulders; about 95 scales from front of shoulders to vent at median ventral line; about 45 scalerows between two well-defined ventrolateral folds; no preanal pores in female but a series of ten enlarged pore-scales in

preanal area, followed by two or three rows of equally large scales; a row of seven or eight larger femoral scales (males with six to ten preanal pores forming a wide angle).

Dorsal surface of body with fine granular scales mixed with about 16 rows of enlarged rounded conical or trihedral scales; tubercles noticeably developed on dorsal part of legs, smaller and inconspicuous on arms; seven or eight lamellae on basal part of longest finger, about ten under longest toe; beyond lamellae the toe bends upward then forward making a distinct crook; underside of base of tail with about 21 small scales; remainder with transversely enlarged scales two to each segment; above, on each segment nine smaller transverse scalerows and a row of four enlarged tubercles placed near posterior part of segment, sometimes two smaller ones preceding these.

Color in life: Above light brown, nearly uniform with a series of four dark-brown bands, bordered or dotted on edges with cream, crossing dorsum and reaching lateral fold; one cream-edged band beginning behind eye runs back and around occiput; venter yellowish cream with a fine powdering of dark pigment, more intense under tail; tail banded in dark brown and tan near base more distally dark bands become black, tan bars become almost white; arms gray-brown, nearly unicolor; legs with numerous cream-colored tubercles. Top of head nearly uniform brown.

Measurements in mm.: Snout to vent, 61; tail (broken), 32; head-width, 12; head-length, 20; snout to arm-insertion, 24; axilla to groin, 29; arm, 23; leg, 31.5.

Remarks: There is considerable superficial resemblance between this species and *Cyrtodactylus pulchellus*. The completely different arrangement of the scales on the femoral and preanal regions together with certain other difference in the relative size and proportions of scales amply distinguish these forms.

The species has been taken in southeastern Thailand, Khao Sebab (mt.) near Chanthaburi, Chanthaburi province, and on the (island) Koh Chang in the Gulf of Siam. Malcolm Smith also reports the species in the Kamchay Mountains in Cambodia.

My specimen was taken at an elevation of about 500 meters on Khao Sebab from under bark of a rotting stump. Only the single specimen was seen.

It seems well to question the locality data (Phatthalung) on a specimen in the Boonsong collection reported by Taylor and Elbel (1958). Certain original tags had disintegrated and others had replaced them.

Genus CNEMASPIS Strauch

Goniodactylus (*non* Kuhl, 1826) Gray, Zoological Miscellany, 1842, p. 58 (type-species, *boiei*).

Cnemaspis Strauch, Mem. Acad. St. Petersburg, vol. 35, 1887, p. 41 (type of genus *Cnemaspis boulengeri*).

Paragonatodes Noble, Amer. Mus. Nov., no. 4, 1921, p. 14 (type of genus, *Gonatodes dickersoni*).

Diagnosis: Digits slender, clawed, not dilated (in Thai species); two distal phalanges compressed, forming an angle with the basal portion of the digit, the lower surface of which has a row of plates; body more or less depressed, granular, or tubercles mixed with granules. Tail more or less cylindrical; pupil round; "eyelid" distinct all around the eye; preanal or femoral pores, or both may be present. Four species of the genus are known to occur in Thailand. They may be distinguished by the following key:

KEY TO THAI SPECIES OF CNEMASPIS

1. Femoral and preanal pores present. Diminutive species with preanal pores widely separated from the femoral pores; some small spine-like scales scattered on flanks ..... *mysoriensis*
   Femoral pores absent; preanal pores normally present 2
2. Base of the raised portion of the digits without one or two thickened plates, these being replaced by small irregular scales. Tail with small keeled scales below; snout with distinct canthal ridges; five transverse yellow bands on body, and the two anterior bright; no large tubercles on tail ..... *affinis*
   Base of raised portion of digits with one or two thickened plates; canthal ridges indistinct or absent; tail with whorls of large tubercles 3
3. Subcaudal area with a somewhat enlarged median series of pointed scales; 2 to 8 pores in preanal region (sometimes abnormally absent); two median rows of tubercles not forming straight lines, *siamensis*
   Subcaudal area smooth with a median series of somewhat rounded scales (not pointed), three to each segment, the third of each group largest; the two median rows of enlarged dorsal tubercles form straight lines; 3-4 minute preanal pores separated mesially by two scales ..... *kumpoli*

Cnemaspis mysoriensis (Jerdon)

Gymnodactylus mysoriensis Jerdon, Jour. Asiat. Soc. Bengal, vol. 22, 1853, p. 469 (type-locality, Bangalore, India).

Gonatodes mysoriensis: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 68; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 77.

Cnemaspis mysoriensis: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 72.

Diagnosis: Small species with from two to three preanal pores, and three to five femoral pores; preanal pores separated from vent by about ten rows of scales; some enlarged scattered scales on dorsum and fine scattered conical tubercles along the flanks; mental large; ear-opening small; diameter of orbit distinctly less than length of snout.

Description of species (from EHT-HMS M 257 (M. S. 4307) from Tasan, Prachuap Khiri Khan): Snout broadly flattened; rostral very broadly visible from above, followed behind by two supralabials and a pair of supranasals; latter separated by a scale nearly as large, which is wedged into notch in rostral and preceded by a short groove; nostril surrounded by rostral, labial, supranasal, and one (possibly two) postnasals; 10 or 11 scales between sutures of first and second labials across snout; while between the fifth labials, 26 to 28 scales; diameter of orbit (2.7 mm.) shorter than snout (3.2 mm.); auricular opening small, diagonal, its distance from orbit, two millimeters; seven supralabials; infralabials 7-7; mental with a larger labial border than rostral, followed by a pair of chinshields, separated by a single scale; a second smaller chinshield also in contact with infralabials, separated from its fellow by three small scales; scales of chin juxtaposed, larger than those of throat; scales on neck, breast, and venter cycloid, strongly imbricating; scales on dorsum and sides larger than occipital scales which are in turn a little smaller than those on snout. A few small tubercles, usually flat, indistinct, with none or but very indistinct keels; a few scattered conical or flattened spiny scales low on sides and in groin area; a pair of preanal pores widely separated by 10-12 scales from a series of 4-3 femoral pores.

Tail with whorls of tubercular spines, six to each basal segment, those low on sides sharpest more nearly erect; subcaudal scales keeled, median series enlarged, but not transversely widened; a large spine at base of tail on each side (small in female); (distal part of tail missing).

Four outer fingers with their basal portions covered with four enlarged flat lamellae, the fourth largest; distal portion of digits compressed, with small scales beneath; toes with large undivided scales under basal part, or with one or two proximal scales divided.

Color: Specimens brownish with numerous small lighter tan spots, especially evident on sides of neck and on digits; tubercles on back light as are the fine spines along sides and in groin; ventral

surfaces much lighter, the throat, breast, underside of limbs, and tail with fine brown pigment; middle of venter without pigment.

Measurements in mm.: Snout to vent, 30; tail missing; width of head, 5.3; length of head, 9.2; snout to arm, 13; axilla to groin, 13.3; arm, 11 ±; leg, 14.5 ±.

Variation: The four specimens all from the same series are dried somewhat and the tails are missing. The measurements are somewhat inaccurate because of drying.

The preanal pores are two in the three males (in one case they are separated mesially by a single scale). The femoral pores are 4-3, 5-5, 5-5.

There may be a broad median yellowish stripe, broken occasionally into spots.

Remarks: It may seem somewhat surprising to find a southern Indian species represented in Thailand. The basis of this record is a series of specimens collected by Dr. Malcolm Smith at Tasan, Prachuap Khiri Khan; Koh Yan Yan, and Koh Lang, islands in the Gulf near the Isthmus of Kra. These specimens were made available to me by Mr. Boo-liat of Kuala Lumpur. The specimens bear Dr. Smith's numbers, within the series 4301-4308, engraved on the characteristic tin tags. I cannot find that he ever reported on these specimens.

The small size of the species; the two or three preanal pores widely separated from the three to five femoral pores; the very large mental as well as numerous other characters make this identification certain.

The specimens have been dried somewhat at some time and are brittle so that accurate measurements of the limbs could not be made.

It is true that there is considerable similarity between *mysoriensis* and *kandianus* and their relationship may be subspecific.

Cnemaspis siamensis (M. Smith)

FIG. 10

Gonatodes siamensis M. Smith, Journ. Sarawak Mus., vol. 3, 1925, p. 21 (type-locality "Maprit, Patiyu", 60 km. N. of the Isthmus of Kra, Thailand); Bull. Raffles Mus. no. 30, Apr. 1930, p. 16; ("Nakon Si Thammarat mountains, Phuket, Krabi, and Tasan in the northern part of the Malay Peninsula. Also in south Tenasserim, Burma and in the mountains near Chantaburi").

Gonatodes kendalli: (*non* Boulenger) M. Smith, Journ. Nat. His. Soc. Siam, vol. 2, 1916, p. 151.

Cnemaspis siamensis: Smith, The Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 71-72.

Diagnosis: Small ground- or rock-dwelling gecko, with numerous rows of enlarged conical, trihedral, or tricarinate scales; ventral scales, cycloid, imbricating, usually tricarinate; mental large, its labial border a third longer than that of rostral; tail slender, somewhat compressed laterally, subcaudal scales enlarged but not trans-

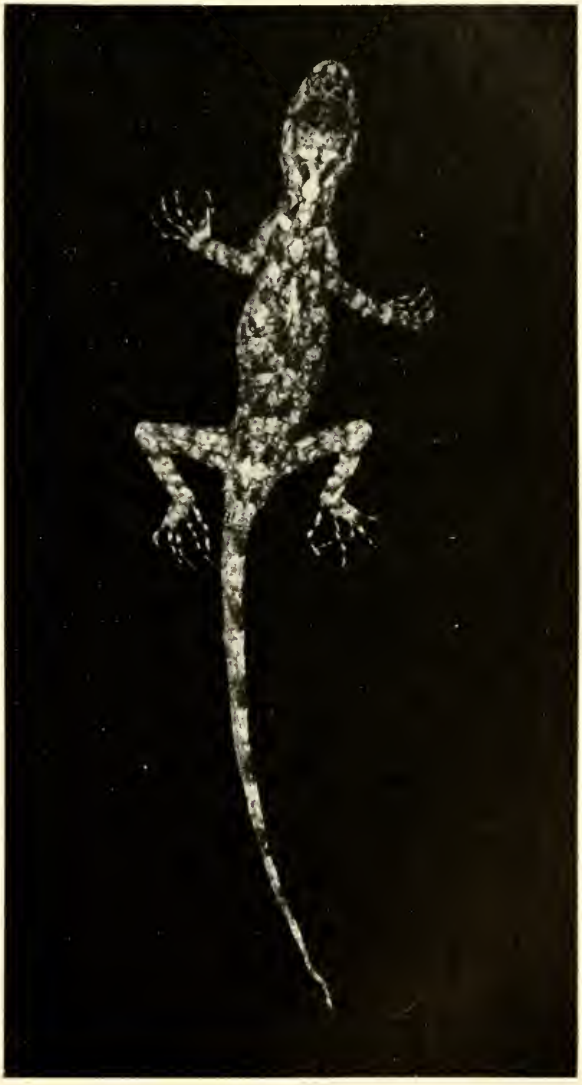


FIG. 10.—*Cnemaspis siamensis* (M. Smith). No. 35696, Khao Chong Forest Experiment Station, Trang province, Thailand. Actual length, 86.2 mm.

versely widened. Most caudal scales, except two or three unicarinate rows, tricarinate (or with two grooves), each segment with 8-10 transverse scalerows, and a row of much enlarged tricarinate tubercles. Preanal pores in male; digits without webs, very slender, all with claws.

Description of species: (from No. 35696, Khao Chong Forest Station, Trang province, Thailand). Snout rather broad, rounded at tip, longer than distance between eye and ear-opening. Rostral large, not twice as wide as high; a large groove or suture enters upper edge and continues down for about four fifths of its height, almost dividing scale; laterally rostral touches first supralabial, posteriorly two supranasals and an internasal; nostril surrounded by rostal, supranasal, and three small postnasals; about 24 scales across snout between mutual sutures of first and second labials; 44 across snout between fifth labials; eight supralabials, anterior ones rather narrow, elongated, and these followed to mouth angle by a row of five or six small undifferentiated scales; ten infralabials, anterior ones wider than long, posterior ones narrow, elongate; mental proportionally very large, its labial border at least a third greater than that of rostral, separating first pair of chinshields, which are a half longer than wide, separated posteriorly by a single scale; two other small scales in contact with labials may represent second and third pairs of chinshields; about 37 scales in a line across interorbital region between middle palpebral scales; a distinct depression behind nostrils; only a slight depression in interorbital and frontal regions, scarcely discernible; scales on occiput smaller than scales on snout, intermixed with somewhat larger tubercles but these much smaller than the 18 or 20 irregular rows of tri-keeled, rounded, conical or trihedral tubercles intermixed with small juxtaposed granular scales on dorsum; no tubercles on limbs, but scales, especially on front side of limbs, strongly keeled, bearing two to four keels; venter covered by about thirty rows of rounded, imbricate, tricarinate scales; female without pores (male with two to eight preanal pores which may sometimes be absent altogether (*fide* M. Smith)); limbs elongate, slender, unwebbed; digits narrow, elongated, and distally slightly compressed; distal phalanges rising from basal part at an angle; basal part of digit with flat lamella the terminal one of each series being an enlarged plate; basal part of distal phalanges with one or two divided scales or a row of small scales; remainder with large plates, or lamellae, a little smaller than those on basal part of digit, 24 to 25 under longest

finger, 25 under longest toe. Ear-opening small, one millimeter in greatest diameter; diameter of the bony orbit of eye about 4.4 millimeters.

Color in life: Above gray-green with darker brown markings; a pair of lines behind eyes converge to a light spot on nape; this light spot preceded by two lighter spots, separated mesially by a small brown spot; two or three lighter areas on side of neck and shoulders. Entire body more or less mottled in brown and light, the brown tending to form transverse bars on back of body; ten bars on tail which cannot be traced to underside of tail. Venter slightly yellowish-white with a peppering under tail of much darker brownish pigment.

Measurments in mm.: Snout to vent, 36.2; tail, 50; total length, 86.2; snout to arm-insertion, 14.1; axilla to groin, 17.2; width of head, 6.5; length of head, 10.7; arm, 16; leg, 21.

Variation: Two males taken in 1960 at Khao Chong are numbered 444 and 390, respectively. The preanal pores are 3-2, separated by a single scale, and 4-4, again separated by a single scale. There are no femoral pores. The median subcaudal scales have single keels and are larger than the adjoining rows.

The pattern of markings is similar in all three specimens. The two pairs of cream marks in front of the shoulders and above the axillae are well marked.

Distribution: The distribution in Thailand is in the southern peninsular part, 60 km. north of the Isthmus of Kra and south, at least as far as Khao Chong, Trang. It occurs also in southeastern Thailand near Chanthaburi.

Remarks: This diminutive species is primarily a rock-dweller but may be found on the buttresses and trunks of trees in the general vicinity of rocks. Several individuals presumably of this species were seen in inaccessible crevices among boulders. The specimen described was caught on a tree buttress growing alongside several large boulders. It was moving about in the morning, suggesting that they are at least partially diurnal in their habits.

These lizards move over the rocks and tree trunks with considerable speed despite the absence of adhesive lamellae. Formerly they were regarded as congeneric with *Gonatodes*. However, the presence of the postanal sacs and true preanal pores are two easily discernible characters that separate them. The digital characters serve as well. In fact they are members of different families.

Gonatodes with its curious scutcheon scales on the venter is placed in the family Sphaerodactylidae, while *Cnemaspis* is placed in the Family Gekkonidae.

The described specimen, contains two equal-sized ovarian eggs. A spider is the only food in the stomach.

Malcolm Smith states that while two to eight preanal pores, in an angular series, is the normal condition, the pores may be absent altogether in males! The pores are not present in females. Smith states that the dorsal tubercles are in "12 or 14 fairly regular longitudinal rows." In this specimen there are 18 or 20 and these are not in regular rows save that they do form indistinct diagonal transverse rows posteriorly.

Cnemaspis affinis (Stoliczka)

FIG. 11

Cyrtodactylus affinis Stoliczka, Journ. Asiat. Soc. Bengal, vol. 39, 1870, p. 167, pl. 10, fig. 1 (type-locality Penang Island, Malaya).

Gymnodactylus affinis: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 42; Flower, Proc. Zool. Soc. London, 1896, p. 862; *ibid.*, 1899, p. 627.

Gonatodes penangensis Flower, Proc. Zool. Soc. London, 1896, p. 863, pl. 44, fig. 1 color, 1a, 1b, 1c, black and white (type-locality, "The Crag" Penang I., elev. 2200 ft., Malaya).

Gonatodes affinis: Flower, Proc. Zool. Soc. London, 1898, p. 455; *ibid.*, 1899, p. 627; Laidlaw, Proc. Zool. Soc. London, 1901, vol. 1, p. 304; Boulenger, Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 149; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 38-39; M. Smith, Journ. Sarawak Mus., vol. 3, 1925, p. 23; Bull. Raffles Mus., no. 3, 1930, p. 16 (Pattani).

Gonatodes kendalli: (*non* Boulenger) M. Smith, Journ. Federated Malay States Mus., vol. 10, 1922, p. 268.

Diagnosis: Snout with canthal ridges, elongate, its length nearly twice diameter of orbit. Intermediate phalanx, between basal and terminal, covered below with small scales; five transverse yellow bands, two anterior very bright, posterior somewhat indistinct; tubercles of anterior band a brilliant golden color; underside of head and on throat orange, the sexes alike in color.

Description of species (from type-description of "*penangensis*"): Habit very slender. Head oval; snout broad and rounded, depressed, with canthal ridges developed, longer than distance between eye and ear-opening, nearly twice diameter of orbit. Eye large. Ear-opening vertically oval. Limbs long; digits long and slender, compressed. Character of scales on lower surface of digits of both hands and feet at once separates this species from *G. kendalli*, in which they are entirely covered with small transverse lamellae, while in this species, through the basal and terminal parts

of phalanges have transverse lamellae, intermediate part is covered with small irregular scales; a large oval plate at articulation of basal and proximal phalanges, as in *G. kendalli;* upper surfaces covered with minute granules, intermixed on body with irregularly arranged small tubercles, bearing slight keels. Rostral large, quadrangular,

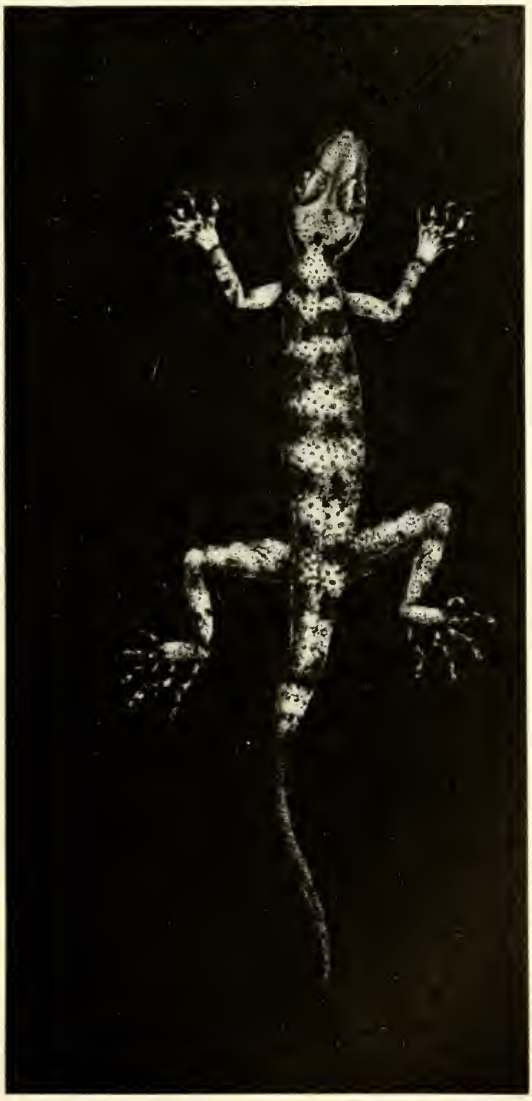


FIG. 11.—*Cnemaspis affinis* (Stoliczka). Figure from Flower, Proc. Zool. Soc. London, 1896, pl. 44, fig. 1 *("penangensis").*

not twice as broad as high, with a median cleft. Nostril between rostral and several small scales. Nine to thirteen upper, and nine to eleven lower labials. Symphysial [mental] very large, subtriangular. Two large chinshields; two or three scales on chin following mental, slightly enlarged. Abdominal scales very small, juxtaposed, convex, keeled. Male with five to seven preanal pores, arranged in an obtusely angular or crescent-shaped line. Tail cylindrical, slender, with small keeled scales and some pointed tubercles; but in none of the four specimens examined is there the series of large spines which are to be seen in some specimens of *G. kendalli.*

"*Colour* (from life): Iris orange or yellow. Above yellowish brown mottled with dark brown; deepest (rich red-dark-brown) on shoulders. Five transverse yellow bands, two anterior very bright; three posterior more or less indistinct in some specimens; tubercles on two anterior yellow bands are of a most brilliant yellow colour. Below, head and throat bright orange, remainder purplish-gray, shading to buff on chest and extremities of limbs. Tail with alternate bands of light and dark brown; in one specimen there are sixteen of these bands, and tubercles on lighter bands white. The sexes seem to be coloured alike."

Measurements in mm.: Total length, 93; snout to vent, 48; tail, 45; head length, 12.5; head width, 7.5; arm, 20; leg, 26.

Distribution: In Thailand the species has been reported from Bukit Besar, Jalor [= Pattani]. It occurs widely in Malaya.

Remarks: Concerning the types Flower states: "I found these Geckos in March 1896, numerous in two small caves in the rocks at the 'Crag,' Penang, at an elevation of 2200 ft. in which they were to be found running over the walls both by day and night; at dusk they could also be found on rocks in the open. They are very active."

Cnemaspis kumpoli sp. nov.

FIG. 12

Type: EHT-HMS No. 3870. Khao Chong, Forestry Experimental Station, Trang province, Thailand. Edward H. Taylor, coll., Sept. 1961.

Diagnosis: First supralabial with anterior portion higher than posterior, the scale excluded from nostril; some posterior supralabials with longitudinal keels; median subcaudal scales smooth, distinctly larger than adjoining rows, only slightly wider than long,

three scales to a tail segment, the third largest of the three; basal tail segments each with a whorl of four large dorsal tubercles, more distally with two or none. Tail and body with transverse bands of blackish gray and light gray; minute preanal pores, 4-3, separated mesially by two scales, separated from vent by six scalerows, and three or four rows of fine granules.

Description of type: Rostral wider than high, depressed somewhat, mesially, with an entrant groove extending more than halfway across scale; a pair of small supranasals, mesially in contact behind rostral; nostril surrounded by rostral, supranasal and three postnasals, the first labial excluded from nostril; a shallow depression behind nostril; snout broad, rather flattened; a broad, very shallow frontal depression; supralabials 11-11, last three small; certain posterior ones with keels; first supralabial higher anteriorly than posteriorly, narrowly excluded from nostril; scales on snout somewhat low, conical or pyramidal, subequal, except for a group of four or five scales a little larger, bordering the supranasals; mental border on mouth a fourth to a third wider than rostral border; the sides of mental notched by first infralabial, truncate behind; a pair of small chinshields touching first infralabils, but separated by a small scale; 10-11 infralabials, first much the largest, diminishing gradually in size, posteriorly, a slight occipital depression; scales in occipital and temporal areas very small, with a few slightly larger scales some distance above ear-opening; scales on dorsum and sides small, subconical, juxtaposed; two mesial rows of tubercles in a continuous line, separated anteriorly by three small granular scalerows, posteriorly, between leg insertions, by about ten rows of granules; on each side of body eight or more irregular rows of tubercles, rather low dorsally, higher and strongly conical, or pyramidal, laterally, practically all showing one or more slight keels; on sides of nuchal region a longitudinal group of large white tubercles; flanks with nearly uniform granules; about 40 rows of small smooth cycloid scales on venter, smaller on throat, larger under femora; a series of very small preanal pores, separated from vent by seven scalerows and three or four rows of granules; scales on arms and legs sharply conical or pyramidal, usually keeled. Tail segmented, subcircular, without fringe, each basal segment with eight or nine transverse rows of granules and a whorl of four dorsal, semierect tubercles, two present laterally; three specialized tubercles on hemipenial swellings; subcaudal scales distinctly larger than dorsal and lateral caudal scales, median row largest beginning with third segment, about 86 in all; tail terminates in a tiny enlargement.

Limbs long, rather slender; digits slender, their basal portion with a row of flat scales or lamellae, the terminal one, a thickened enlarged plate; from this, the distal angular part of digit arises; this part with a series of lamellae below, usually single, rarely

FIG. 12.—*Cnemaspis kumpoli* sp. nov. EHT-HMS No. 3870, Khao Chong Forestry Experiment Station, Trang province, Thailand. Snout-vent length, 52 mm.; tail-length 68 mm.

divided; all scales and lamellae under fourth toe total 32; adpressed leg reaches to or very near to ear-opening; the arm adpressed reaches to groin; ear-opening nearly vertical, its diameter, approximately 1.1 mm., less than one third of the diameter of orbit.

Color in life: Above generally olive-gray with dark or blackish gray transverse bars on body; a horseshoe-shaped mark from eye to eye extending around occiput bordered by an olive-gray lighter line; two black nuchal marks each bearing a series of enlarged white tubercles; four broad dark bands on body, separated dorsally by bands of gray that narrow much on sides; tail banded in blackish gray and light gray the bands encircling the tail; limbs dimly barred with grayish brown; digits distinctly barred with dark and light gray; chin and venter dirty grayish white each scale with a peppering of darker pigment.

Measurements in mm.: Snout to vent, 52; tail, 68; snout to arm-insertion, 20; axilla to groin, 24.5; width of head, 10; length of head, 13.7; arm, 23; leg, 31.

Distribution: Known only from the type locality.

Remarks: The type was captured at night while collecting with Dr. Robert Elbel, near the forestry shelter house at Khao Chong, Trang province. It was running about on a tree trunk. The key will distinguish it from other Thai species of the genus.

The species is dedicated to Nai Kumpol Isarankura, Curator of Zoological Collections at Chulalongkorn University, Bangkok Thailand, who has been very helpful to me in my study of the Thai faunas.

Genus PHYLLODACTYLUS Gray

Phyllodactylus Gray, Spicilegia Zoologica, 1828, p. 3 (type, *Phyllodactylus pulcher*).

Digits clawed, slender, distal phalanges not elevated, with a pair of widened terminal plates separated mesially by a groove into which the claw is retractile; preanal pores absent in Western Hemisphere forms, present or absent in Asiatic, Australian, and African forms. Body covered with small scales, uniform or mixed with conical or trihedral tubercles arranged usually in longitudinal rows; pupil vertical.

Two species of the genus occur in Thailand. They may be differentiated by the following key:

KEY TO SPECIES OF PHYLLODACTYLUS IN THAILAND

Body above with numerous rather large black spots (rarely diffuse); tail banded dark and light; no black stripe from tip of snout through eye to tail; usually six preanal pores; lips strongly barred with cream and black ..... *siamensis*

Dorsal spots absent or minute if evident, arranged in four longitudinal lines; a black stripe from tip of snout to tail bordered above by a cream-white stripe to shoulder; labials whitish. Nine preanal pores, *melanostictus*

The genus *Phyllodactylus* as now understood, is distributed widely over the earth in Asia, Australia, and Africa and in tropical and subtropical parts of the Western Hemisphere. Four species are known to occur in Asia: two species in Persia and two in southeastern Asia. There is no evidence to show that the distribution of the genus is continuous in Asia.

There is no certainty that the species occurring in Asia, Africa, and Australia are generically identical with those in America since skeletal and perhaps other significant structures have not been scrutinized. The terminal digital lamellae are similar to those in the Western Hemisphere, but all these, in fact all endemic Western species belonging to the Gekkonidae, lack femoral pores. This latter character is, however, variable in old world *Phyllodactylus*.

The Thai species are completely terrestrial and males have femoral pores. That they are not to be regarded as subspecies is evidenced by the occurrence of both species in Muak Lek, Sara Buri province. Each maintains its own identity, *siamensis* occurring over most of Thailand, while *melanostictus* is known only from the type locality in Central Thailand.

Phyllodactylus siamensis Boulenger

FIG. 13

Phyllodactylus siamensis Boulenger, Proc. Zool. Soc. London, 1898, p. 918, pl. 55, figs. 1, 1a (type-locality, Dong Paya Fai Mts., eastern Thailand); Flower, Proc. Zool. Soc. London, 1899, p. 627; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916, p. 52 "Widely distributed; extending into the peninsula as far south as Bangsaphan, Lat. 11° 13′"; Bull. Raffles Mus., no. 3, 1930, p. 20; Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 10; Bourret, Bull. Gen. Publ. Inst. no. 19, 1939(?), p. 51 (South Annam).

Phyllodactylus pavici Mocquard, Mission Pavie Indo-China, 1879-95, Lizards, 1904, p. 486, pl. 23, fig. 3 (type-locality Vatana [= Wattena], Thailand).

?*Phyllodactylus burmanicus* Annandale, Ann. Mag. Nat. Hist., ser. 7, vol. 15, 1905, p. 28 (type-locality, Tavoy, Burma).

Diagnosis: A small species reaching 52 mm. snout to vent. Terminal part of digits with a pair of widened lamellae; dorsal part of widened area covered with eight or ten scales; a median series of

three or four rows of fine scales on body, flanked on each side by seven or eight rows of keeled trihedral tubercles, the three median dorsal rows separated by at least one row of tiny scales; laterally smaller granules surround keeled scales; lateral scales gradually changing into the somewhat larger cycloid ventral scales, each with a distinct but minute posterior serration; six preanal pores in a curving (or broadly angular) series; scales on tail segments arranged in whorls, usually three transverse rows on each, the posterior row being of large keeled scales; subcaudals widened; young black, with a lateral row of small yellow spots; head, back, and sides with numerous well-defined black spots; lacking a dark stripe from rostral through eye to tail, bordered partly with white.

FIG. 13.—*Phyllodactylus siamensis* Boulenger. From left to right: No. 34267, Bang Saen, Chon Buri; length 94.5 mm.; No. 34269, Bang Saen, Chon Buri, length 95 mm.; No. 35035, mountains east of Udon Thani, Thailand; length, 99.5 mm.

Description of species (from No. 33575, Ang Hin, Chon Buri province): Rostral large, quadrangular, with an entrant suture from above partially dividing scale; a pair of enlarged internasals, each followed by a smaller scale, the pair separated by two granules; nostril surrounded by rostral, two internasals, first labial, and two small postnasals; pupil of eye vertical; "eyelid" visible above eye and palpebral scales on its anterior upper border largest; auricular opening large, its diameter about half of diameter of eye; eight supralabials, sixth below pupil; six infralabials, fifth below eye.

Border of mental on lip larger than that of rostral; mental scale rounding anteriorly, forming a right angle posteriorly; pair of enlarged chinshields touching one labial and forming a median suture at least half as long as the scales; second pair of chinshields smaller, touching first and second infralabials, separated from each other by two small scales; scales on chin granular, gradually increasing in size, becoming as large as ventrals on back part of neck; 23 scales across snout between third supralabials; about 26 granules between median points on palpebral series; a few small tubercular scales intermixed with occipital and temporal granules; rows of trihedral scales begin behind occiput, at first small, growing larger on dorsum; two median series separated on median line by from two to four rows of granules (usually 3), each tubercular scale separated from next in line by small granular scale. Lateral tubercular scales surrounded by small granules, or touching each other at certain points; ventral scales subcycloid, their posterior edges with a fine but distinct serration seen under a lens; dorsal trihedral scales becoming smaller laterally and gradually merging into ventral scales.

Tail cylindrical with rather indistinct segments, each with three transverse series of scales above (posterior series largest) and each with two subcaudals; subcaudals, 58, each with a distinctly serrated edge posteriorly; six rows of scales between first enlarged subcaudals and vent.

Limbs well developed, clawed, pentadactyl, with a pair of widened terminal lamellae, between or just anterior to which claw is partially or completely retracted; five scales on dorsal part of terminal expansion; 11 undivided smooth lamellae under longest fingers, 12 to 13 under longest toe; (male with eight preanal pores in a curving or broadly angular series). Underside of upper part of arm and posterior part of thigh with fine granules; remainder of limbs with imbricate scales, many of those on legs, at least, being keeled and trihedral in shape.

Color in life: Above somewhat lavender-brown to grayish; an indistinct dorsolateral series of 17 pinkish, buff, or yellowish dots beginning at occiput and extending to tip of tail; venter with a dull yellowish wash; tail gray below, heavily flecked with brown. Occiput with two or three curving dark marks; body with numerous scattered black spots; an irregular dark area on postorbital region; sides flecked with black; tail with blackish spots which toward end tend to form transverse bands in front and behind yellow spots which themselves form bands near the tail tip; supra- and infralabials cream with dark spots; a few dark markings on head.

Measurements in mm. of *Phyllodactylus siamensis*

NUMBER†	36084	36033	34978	34979	496
Snout to vent	53	48	50	46	45
Tail	52.5*	51*	47*	50.3	36*
Snout tip to arm insertion	21	19	21.2	18	17.8
Axilla to groin	24	22.5	24	22.5	22
Width of head	10.2	10	10.8	9	10
Length of head	16	14.2	15.2	15	15.2
Arm	16	15.8	15.2	13	14
Leg	21	20.6	21.4	18.6	19

†36084, 36033, Kaeng Pang Tao, Chiang Mai; 34978, 34979, Nong Boa Lumpoo, Loei; 496, Songkhla, Songkhla.

* Tail regenerated.

Distribution: This widespread species appears to be distributed over the entire country with the exception of high mountainous areas. Malcolm Smith has reported the species as far south as 10° lat. Whether its distribution has been facilitated towards the south by the presence of the railway as suggested by Dr. Smith may be doubted since it occurs on islands in the Gulf of Siam. However, the southernmost record (my own) at Songkla (latitude 7°) is from a point only about 200 meters from the railway. The species occurs in South Annam and if *burmanicus* is correctly synonymized here, it is also to be found in Burma.

Remarks: Differences in various populations of *siamensis*, while not great are such that a population may be recognizable on the basis of certain small scale or marking characteristics.

Phyllodactylus melanostictus Taylor

FIG. 14

Phyllodactylus melanostictus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 215-218, fig. 3. Type-locality, Mauk Lek Road-Camp, Friendship Highway, Sara Buri (practically on border of Sara Buri and adjoining province, Nakhon Ratchasima).

Diagnosis: Differs from *Phyllodactylus siamensis* in having a black stripe from tip to snout through eye to shoulder where it widens and continues along side of body and then narrows on tail. Dorsal spots if present very small, arranged in four longitudinal lines; a series of small dots on dorsal part of tail; arms and legs colored like sides of body; no white rings on tail.

Rows of enlarged trihedral or keeled tubercles present, median rows smaller than other rows, separated by three rows of small granules; next two rows separated by one row of granules; nine preanal pores in males.

Description of type: Rostral large bordering nostril, subquadrangular, wider than high, with a median entrant suture in upper mesial part; a pair of enlarged internasals forming a straight median suture, and forming part of border of nostril; behind internasals another slightly enlarged pair of scales; first labial and two tiny postnasals form remainder of border of nostril; 29 scales in a row across head between edges of eyelids, and 28 scales in a row across snout between posterior edges of third labials; scales on snout slightly larger than those on interocular and occipital regions; granules in temporal areas slightly larger, with some still larger scales intermixed. Nine supralabials, seventh directly below pupil of eye; seven infralabials, fifth below pupil of eye; auricular-opening small, little larger than an internasal scale; mental with larger labial border than rostral, its posterior sides forming a right angle; a median pair of enlarged postmentals, each followed by two smaller widely separated pairs of scales; granules on chin and throat very small, subequal.

Dorsum covered with rows of trihedral or bluntly keeled tubercles, two rows near middle separated by three rows of small granules; next row separated from these by an irregular row of granules; subsequent rows contiguous or with only a few scattered granules between them; about ten or eleven rows on sides and dorsum but there is no distinct line of demarcation between these and flat cycloid scales of venter; latter scales in about 22 rows. A curving row of nine preanal pores; subcaudals enlarged, widened. Two postanal swellings indicate position of hemipenes; two rounded tubercles arising from each swelling. Limbs well developed, each digit with paired leaflike lamellae at tip, between which may be seen a small retractile claw; when limbs are adpressed, toe reaches halfway to elbow. Ten lamellae under longest fingers; fifteen under fourth toes, distal one usually divided. Segments of

tail distinct each segment with three or four transverse rows of scales arranged in whorls; posterior row with at least four enlarged keeled scales; on underside of each whorl, two subcaudals, anterior the larger (a total of about 30 segments in a complete tail).

Color in life: Above lavender-gray, top of head lighter, mottled with some darker color; a moderately distinct cream-white stripe from tip of snout through eye, disappearing on shoulder; bordering this below a black stripe extending from tip of snout onto tail, widening on sides and less distinct; labials and side of neck below stripe, white. Chin, throat, and venter white but under a lens fine

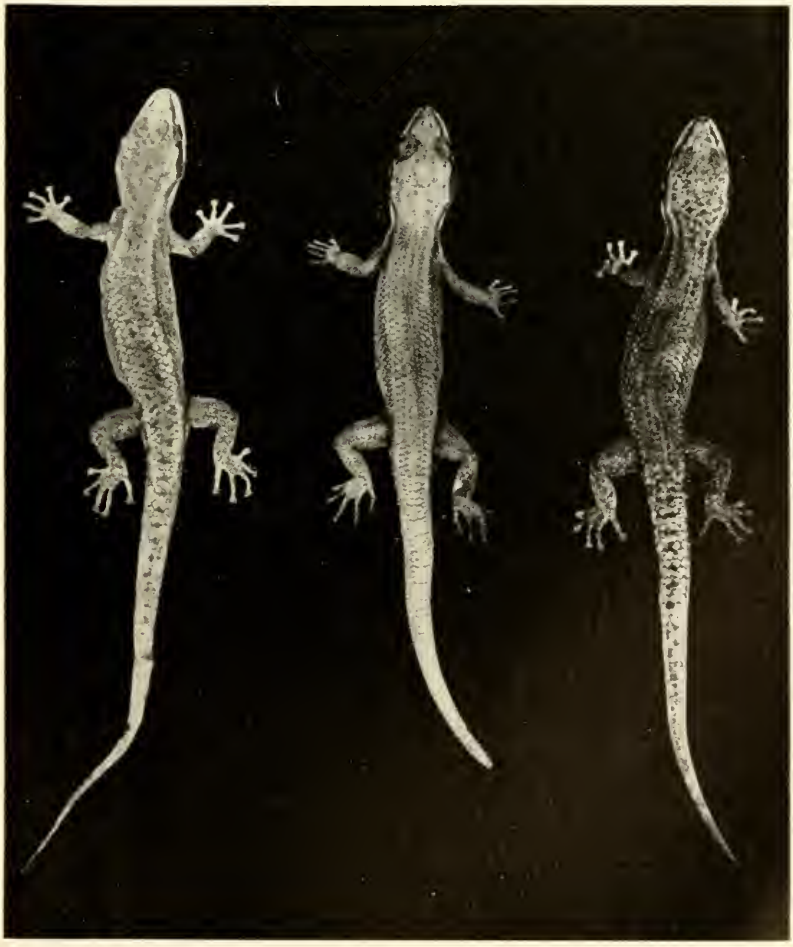


FIG. 14.—*Phyllodactylus melanostictus* Taylor. Fig. from Taylor, Univ. Kansas Sci. Bull., vol. 42, 1962, fig. no. 3.

pigmentation evident, less on chin than on venter; latter half of tail regenerated; basal part with a series of black spots marking segments.

Measurement in mm. (of type, No. 33333 ♂): Snout to vent, 42.5; tail, 54.5; total length, 97; snout to arm-insertion, 18.5; axilla to groin, 19; arm, 12; leg, 17; head width, 8.2; head length, 12.8.

Variation: The following variation is evident: No. 33334: The dorsum is lighter than in the type and the stripe on the side of the body is dimly evident. The entire tail has only vague lines marking the segments. There are nine preanal pores. There is no spotting or reticulation on head or body except two or three dark spots on labials.

No. 33331 ♀: The dorsolateral light stripes can be traced to tail as a series of dots. The pigment on the back is segregated into dark flecks forming four fine broken lines while the median line is nearly as light as the dorsolateral line. The head has numerous brown-lavender flecks. The labials have more distinct spotting, and the subcaudal region is darker.

No. 33332 ♀ resembles No. 33334. The tail is missing, and the lateral body stripe is more distinct.

Remarks: The specimens were taken from under logs or boards on wet earth. *Phyllodactylus siamensis* was taken less than 300 meters away. All specimens are from Muak Lek Road-Camp, near the town of Muak Lek, on the Friendship Highway, and actually less than three hundred yards from the boundary between the provinces of Sara Buri and Nakhon Ratchasima (Korat).

Variation: The type and paratypes are all generally similar as regards color and markings.

Distribution: It would appear that this form has originated and is still confined to the central mountain range in Sara Buri, and Nakhon Ratchasima provinces. This range is sometimes known as the Dong Paya Fai Mts. This area is also the home of such endemic species as *Riopa koratensis*, *Cyrtodactylus angularis*, *Riopa parietalis*, etc.

Genus HEMIDACTYLUS Oken

Hemidactylus Oken, Isis, 1817, p. 1183 (type of genus, *Gecko tuberculosus* = *Hemidactylus mabouia*).

Diagnosis: Relatively small species, the digits having widened lamellae divided mesially below on proximal part, all bearing clawed distal phalanges arising angularly from widened portion of

digit; digits without webs. Most species with small granular scales sometimes intermixed with larger tubercular granules; pupil vertical; preanal and/or femoral pores.

While the genus has some 70 species and is widespread in Asia, Africa, and Polynesia, the genus is represented in Thailand by only two species. These are *Hemidactylus frenatus,* an ubiquitous species, one of the two commonest "chinchooks" in Thailand, and equally common in trees and houses. The second is *Hemidactylus garnotii,* a widely distributed forest form, and more rarely a domestic species, that has a preponderance of females, the males being exceedingly rare. Dr. Malcolm Smith (1935) states that he has seen more than 100 specimens and has never seen a male. The species is rarely to be found in houses in Thailand. However, I took one at Khao Chong, Trang, in a forest rest-house, and several in a dwelling house in northern Thailand. *Hemidactylus frenatus* has been accidentally transported to Acapulco, Mexico (probably from the Philippines in Spanish times), and is now rapidly becoming distributed along the highways. It is presumably confined to houses, since I have never found the species in forested areas in Mexico, and presume that it cannot compete with the forest geckoes or other lizards.

Key to Thai Species of Hemidactylus

Tail not or scarcely flattened, with whorls of erect tubercular spines on each segment; without lateral denticulations. Males as numerous as females ..... *frenatus*

Tail flattened, with flat imbricating scales, lacking erect tubercular spines; edges of tail denticulated. Males unknown in Thailand ..... *garnotii*

Hemidactylus frenatus Schlegel, in Duméril and Bibron

Fig. 15

Hemidactylus frenatus Schlegel, in Duméril and Bibron, Erpétologie Générale, . . . vol. 3, 1836 (type-locality, Java); Günther, The reptiles of British India, 1864, p. 161; Boulenger, Catalogue of the lizards in the British Museum, 2nd ed., vol. 1, p. 120; Fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 85; Flower, Proc. Zool. Soc. London, 1899, p. 628; Mocquard, Les reptiles de l'Indo-Chine, 1907, p. 29; Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 4, Dec. 1915, p. 238 ("Klong Yai"); *ibid.,* vol. 2, no. 1, June 1916, p. 52 (common almost everywhere); The fauna of British India including Ceylon and Burma; Reptilia and Amphibia; vol. 2, Sauria, 1935, pp. 95, 96, fig. 29. (The literature list of this species is very extensive. Only a few titles are given.)

Diagnosis: Body covered with small granules intermixed with a few scattered rounded smooth or feebly keeled, conical tubercles; male with a continuous series of preanofemoral pores, 14-19 on each

side; two pairs of postmentals, the outer pair nearly as large as inner, both touching labials; whorls of elevated spiny tubercles on tail.

Description of species (from No. 33715, Chiang Mai): Head slightly distinct from neck; rostral quadrangular, its width (2.75 mm.) much wider than high (1.8 mm.); a median suture in upper part (1.1 mm.), bordered laterally by first supralabial and mesially by two supranasals and a median internasal; nostril surrounded by rostral, supranasal, two postnasals, and first supralabial, its rim somewhat elevated; 12-12 supralabials, last three small, followed by ten or eleven granules to mouth-angle; eight or nine infralabials; mental triangular with a labial border larger than that of rostral; two pairs of chinshields, first forming suture behind mental; second chinshields border infralabials but separated behind first pair by five rows of granular scales; scales following second pair somewhat enlarged; a shallow frontal concavity extending back and onto occiput; auricular opening diagonal (1.7 mm. long), its distance from orbit (5.5 mm.) less than distance from orbit to tip of snout (6.5 mm.); diameter of orbit four millimeters; 21 scales across snout between second labials, 41 between fifth labials; scales on snout, on side of neck and body granular, subconical, juxtaposed, larger than granules in interorbital, occipital, and median dorsal areas; back with two rows of larger flat tubercles separated by four rows of fine granules; dorsolaterally two similar irregular rows of larger tubercles and a few scattered ones; segments of tail well marked, each limited by a whorl of six strong elevated spiny tubercles, the ventrolateral series largest; each whorl with ten or eleven rows of subcycloid granular scales imbricating somewhat; extreme tip of tail regenerated; subcaudal scales except at base of tail transversely widened into plates, two associated with each segment. Scales on chin small, juxtaposed; scales on throat, breast, venter and under thighs larger, cycloid, imbricate, but not entirely uniform in size; two indistinct ventrolateral folds with about 32 rows of scales between. A continuous row of 29 femoropreanal pores 14(15) on each side, median pores largest.

Digits unwebbed, with proximal parts covered below with widened, slightly diagonal lamellae, five under inner (smallest) finger, seven or eight under others, all paired except distal and most proximal ones; the two distal phalanges (with claws) compressed, elevated at an angle, reaching forward from tip of widened part.

Toes unwebbed, with similar lamellae, five on shortest, nine

FIG. 15.—*Hemidactylus frenatus* Schlegel, in Duméril and Bibron. Left figure, No. 33715. Chiang Mai, Chiang Mai province, Thailand. Actual length, 119.5 mm. Right figure, No. 33719, same locality. Actual length, 120 mm.

on longest toes; hand and foot with larger imbricating cycloid scales on upper surface, and on anterior face of arm.

Color: The color brownish gray clouded or flecked with darker gray; yellowish or yellowish-white on ventral surfaces; lamellae dark gray to lavender.

Measurements in mm.: Snout to vent, 57; tail, 62.5; width of head, 12; length of head, 16.5; snout to arm-insertion, 21; axilla to groin, 28; arm, 16; leg, 21.

Variation: Living specimens usually have a fairly distinct color pattern often consisting of a dark gray stripe on side of head, neck, and body; a tail banded in dark and light gray; a dorsolateral dark stripe, somewhat sinuous anteriorly, enclosing a series of discernible light gray spots or dashes. A similar median stripe usually also present. The tail is somewhat pigmented below. There are variations in dorsal squamation, the two principle ones being:

1. Two median rows of distinct widely spaced tubercles, the two dorsolateral ones somewhat irregular.
2. No median rows present, the lateral tubercles reduced to one row with a few scales representing a second.

These may occur in the same population and both extend from the northern to the extreme southern part of Thailand. The character of the femoral pores differ, some specimens having them cut across the scale as an elongate slit. In others the scale pores may be oval, or the median ones slitlike, the others rounded. The number of femoropreanal pores varies between 28 and 36. Occasional specimens have a small third pair of chinshields.

Distribution: Found everywhere in Thailand except perhaps in high mountains. The species is widespread in south and eastern Asia, in the Indo-Australian Archipelago, the Philippines, some oceanic islands in the Western Pacific and Indian Ocean, and in east Africa.

Remarks: Eggs of *Hemidactylus frenatus* are usually placed under bark stuck on tree trunks or placed in crannies in walls or other objects. When the young hatch they are dark blackish-brown in color with numerous bright golden spots arranged in a dorsolateral line. Shortly after emerging from the brittle shell and after becoming dry, the epidermal skin becomes loose. The behavior of one young was observed. By rubbing its nose against some object the skin was rubbed loose and pushed back. Then the young animal turned its head back seizing the loose skin on the shoulder and breaking it. It then pulled it away and proceeded to eat it. This

was continued until all the skin was removed from body and limbs, and all of it consumed. Only that on the tail now remained. This was seized near the base and pulled wrong-side-out and left for some time hanging to the tip of the tail. Finally this was caught up and swallowed, finishing the task. The whole time consumed was approximately 12 minutes. Other young have been watched and the process of removing the loose skin was much the same except the order in which various portions were removed. This seems to constitute their first meal.

Hemidactylus garnotii Duméril and Bibron

FIG. 16

Hemidactylus garnotii Duméril and Bibron, Erpétologie générale . . . vol. 3, 1836, pp. 368-369 (type-locality, Tahiti); Boulenger, Proc. Zool. Soc. London, 1883, p. 118, pl. 21, fig. 1; Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 141; The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 94; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 315; Stejneger, Proc. U. S. Nat. Mus., vol. 21, 1899, p. 792, fig.; Laidlaw, Proc. Zool. Soc. London, vol. 1, 1901, p. 305; Annandale, Ann. Mag. Nat. Hist., ser. 7, vol. 15, 1905, p. 30; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 6, 1923, pp. 196-197 (Hainan); Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 100-101.

Doryura gaudama Theobald, Journ. Linnean Soc. London, vol. 10, 1868, p. 30 (type-locality, Tonghu [valle Sittangensi], Burma).

Hemidactylus gaudama: Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, p. 288.

Diagnosis: The slender compressed joint of inner digits at least half as long as dilated portion; enlarged dorsal tubercles along flanks, rounded, moundlike, or conical; tail flat below, edges finely denticulated; segments rather distinctly marked; median subcaudals widened; second pair of chinshield separated from infralabials normally.

Description of species (from No. 36134, Chiang Mai): Head rather slender, body flattened; rostral not quite twice as wide as high, upper part tending to flatten out on top of snout; a median suture passes forward from upper edge nearly half way across scale; rostral followed by a labial on each side, and two supranasals separated by one scale; nostril surrounded by rostral, first labial, supranasal, and two small postnasals; eleven supralabials followed to angle of mouth by five or six small scales; about 43 scales in a line between back edge of fifth supralabials across snout, those on sides a little the larger; some larger scales bordering supralabials; about 42 small granules between outer edges of eyelids counting in a line crossing at middle of eyelids; mental with a labial border about equal to that of rostral, followed by two pairs of chinshields, anterior

FIG. 16.—*Hemidactylus garnotii* Duméril and Bibron. Left figure, No. 36134, Doi Suthep, Chiang Mai province; total length, 119.5 mm. Right figure, same locality?; total length, 122 mm.

only touching labials and forming a mutual suture less than half their length; second pair separated from supralabials by a row of small scales and separated from each other by two small scales; 9-10 infralabials; one or two irregular rows of slightly enlarged scales border infralabials; diameter of orbit equal or slightly less than its distance from nostril.

Scales on snout larger than occipital scales or those on middle of dorsum; on sides of body scales larger than on dorsum with numerous scattered tubercles that are somewhat larger than other scales, most prominent dorsolaterally on latter half of body; two prominent ventrolateral glandular folds; between these, scales in about 30 rows, cycloid, imbricating, their posterior edges distinctly serrate; small granules on chin, becoming imbricate on throat.

Tail flattened below, elevated above, edged with a fringe of scales, every fourth or fifth one larger marking the segments of tail; scales above somewhat cycloid imbricating; strongly widened subcaudal series, usually two to each segment; regenerated tail also with widened scales but fringe scales are nearly uniform; fingers and toes widened with compressed terminal portion rising above the widened lamellar portion, all with claws; paired lamellae under fingers except basal ones may be single, as is the terminal one at distal end; toes with similar lamellae; a slight web-remnant present; inner finger and toe short, narrow, with a well-developed distal compressed joint with claw. A series of femoral scales extending onto preanal region; ten scales of femoral region on each side bear pits or perforations, these series separated by eight intervening preanal scales that lack pits.

The area at base of subcaudal region swollen with a single small lateral tubercle on each side.

Color: Above uniform fawn to gray fawn; venter creamy yellow; lamellae dark under digits. There are no pigment dots on ventral scales save a few on infralabials and on outer subcaudals.

Measurements in mm. of Nos. 36134 ♀ *and 35978* ♀ : Snout to vent, 57, 64; tail, 62.5, 82; snout to arm-insertion, 22.6, 25; axilla to groin, 28, 28; width of head, 11, 13; length of head, 16, 16.3; arm, 18, 20; leg, 21, 25.

Variation: Most specimens have a slight frontal concavity, in others this is scarcely indicated. One specimen from Chiang Mai has the dorsal parts brownish gray with 9 or 10 transverse series of rounded whitish spots tending to form two longitudinal lines as well. One or two rows may continue on the tail. Arms and legs

likewise marked with bands of white marks. A specimen from Kaeng Pang Tao has an indistinct lateral band of dark gray and three dorsal series of elongate spots forming three broken dorsal stripes; some spots on basal part of tail white, the latter two thirds is distinctly banded in light and dark gray bands. This specimen has both pairs of chinshields touching labials.

Specimens from Trang have whitish spots on the body, and on one the tail is banded.

Some specimens show large deposits of calcium about the ear region. One specimen from Trang is badly infested with segmented worms. These are subcutaneous their length being from ten to 16 millimeters.

Distribution: It seems probable that there has been some confusion with regards the identification of this species. The absence of male specimens from collections can scarcely be explained save on the possibility of parthenogenesis which seems too improbable to be considered. The type locality of *garnotii* is Tahiti.

In Thailand I have taken specimens from the provinces of Chiang Mai, and Trang.

Taylor (1934) reported the species from Chiang Mai under the name of *Hemidactylus gaudama.*

Outside of Thailand the species (presuming the Thailand form has been correctly identified with *garnotii*) is widespread in Malaya, Indo-Australian Archipelago, and to Tahiti, its type locality.

Remarks: I have found no males of this species in Thailand. Malcolm Smith (1935) reports that he has seen more than 100 Thai specimens of this species but has never seen a male.

It would appear that *Doryura gaudama* Theobald was based on a male having 38 femoral pores, 19 on each side in a slightly curved series. I have seen a male from the Philippines with pores.

Genus PLATYURUS Oken

Platyurus Oken, Algem. Naturgesch, vol. 6, 1836, p. 641 (type-species *Hemidactylus marginatus*).

Cosymbotus Fitzinger, Systema Reptilium, 1843, pp. 19, 104 (type-species *Hemidactylus platyurus*).

Mimetozoon Boulenger, Proc. Zool. Soc. London, 1896, p. 767 (type-species *floweri*).

The name *Platyurus* for this genus of lizards was used by Oken in 1836 and so far as known is the oldest. However, because of the similarity of this name to *Platurus* of Latreille it was rejected.* Fitzinger proposed the name *Cosymbotus* in 1843 in Systema rep-

* See Stejneger, Bull. 58, U. S. Nat. Mus., 1907, p. 178.

tillium (type *platyurus*) and this available name was used by many authors. However, Malcolm Smith revived *Platyurus* for this genus in 1935.**

The present nomenclatorial rules admit generic names that have the same meanings, derived from the same Greek or Latin words providing they differ by a single letter. Thus the name *Platyurus* will stand.

Diagnosis: Digits webbed, the terminal phalanges (with claws) arising free from middle of widened portion of digits; basal phalanges with lamellae, paired, slightly diagonal, except first and last which are single; no digits without terminal phalanges and claw; a cutaneous fringe from axilla to groin and on sides of tail; no tubercles on body or tail; subcaudals widened.

The genus is widely distributed, probably very largely through man's agency since the species seems to prefer human dwellings.

The differences between the genera *Platyurus* Oken and *Mimetozoon* Boulenger appear to be differences chiefly of degree and consequently the two are here treated as a single genus with two species occurring in Thailand.

Key to Thai Species of Platyurus

Body with a narrow lateral fringe or skin-flap from axilla to groin; no fringe on side of head and neck; tail with a narrow denticulated fringe ..... *platyurus*

Body with a broad lateral fringe from axilla to groin; a fringe on side of head; tail with a broad denticulated fringe ..... *craspedotus*

Platyurus platyurus (Schneider)

Fig. 17

Stellio platyurus Schneider, Amphibiorum physiologiae specim., vol. 2, 1797, p. 30 (type-locality, unknown); Denksch. Akad. Munich, vol. 3, 1811, p. 62, pl. 1, fig. 3.

Nycteridium platyurus: Stoliczka, Proc. Asiat. Soc. Bengal, 1871, p. 194; Journ. Asiat. Soc. Bengal, 41, (2), 1872, p. 103.

Hemidactylus platyurus: Boulenger, Catalogue of the lizards of the British Museum, 2nd Ed., vol. 1, 1885, p. 143; The fauna of British India, . . . Reptilia and Batrachia, 1890, p. 95; Flower, Proc. Zool. Soc. London, 1899, p. 629; De Rooij, Reptiles of the Indo-Australian Archipelago, vol. 1, Lacertilia, Chelonia and Emydosauria, 1915, pp. 34-36, figs. 23, 24; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 53, and no. 2, Dec. 1916, p. 152 (Maprit, and Klong Bang Lai, Chumphon) ("Common almost everywhere").

Cosymbotus platyurus: M. Smith, Bull. Raffles Mus., no. 3, Apr. 1930, p. 19; Taylor, The lizards of the Philippine Islands, 1922, p. 59; Deraniyagala, Ceylon Journ. Sci., sec. B, vol. 16, 1932, p. 306; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, p. 1082 (Rat Buri province).

Platyurus platyurus: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 102-103.

** Fauna of British India . . . vol. 2, Sauria, p. 102.

Diagnosis: Digits webbed and dilated; lamellae under toes divided; distal phalanges long, slender (with claws) arising at an angle from above widened portion of digit-tip; two pairs of postmental chinshields, second pair lateral to larger inner pair; a distinct skin-fringe from axilla to groin covered with small scales; a broad cutaneous fold along back edge of leg; 16-20 preanofemoral pores in a continuous series on each side, meeting mesially.

Description of species (from No. 35983, Chiang Mai, city): Head moderately slender; width of rostral (2.4 mm.) much less than twice height (1.6 mm.); bordered by one labial, laterally and by a pair of supranasals and a small internasal posteriorly; nostril surrounded by rostral, supranasal, first supralabial and two postnasals; 12 supralabials; eight or nine infralabials; mental rather large, its labial border equal to that of rostral, followed by a median pair of chinshields, flanked by a second pair; first chinshields in contact for about half their length, second pair separated by two or three small scales.

Scales on snout juxtaposed, slightly conical, larger than other scales on dorsal and lateral parts of body; scales on chin cycloid juxtaposed, becoming imbricate on throat and breast; a lateral fringe on sides of body from axilla to groin, its width two millimeters at widest point; scales on venter larger, cycloid, imbricate, their back edges often with a fine serration; front and ventral surface of femur and tibia with cycloid imbricate scales equal in size to scales on venter; posterior row of scales on underside of femora bear pores (in male), totalling about 36; no large tubercles on postanal swellings in male or female; a fringe on posterior part of thigh and tibia; a slight lateral fringe on sides of tail; subcaudal scales, except at base of tail, widened, two to each segment; outer edge of tail serrate, segments marked by a pair of larger denticulate spines, one on each side, in the fringe on tail.

Digits of hands and feet nearly half webbed, except between the two outer toes where there is less web; digits widened with paired lamellae below; distal phalanges (with claws) arise from middle of expanded tip at an angle and extend forward beyond widened part, not attached to it by a web; inner digits small, but distal phalanges and claws present; six paired lamellae under most of longer digits; the distal and often proximal one, single.

Color: Above varying shades of gray; usually a pattern is visible (it can appear and disappear in living specimens) consisting of a

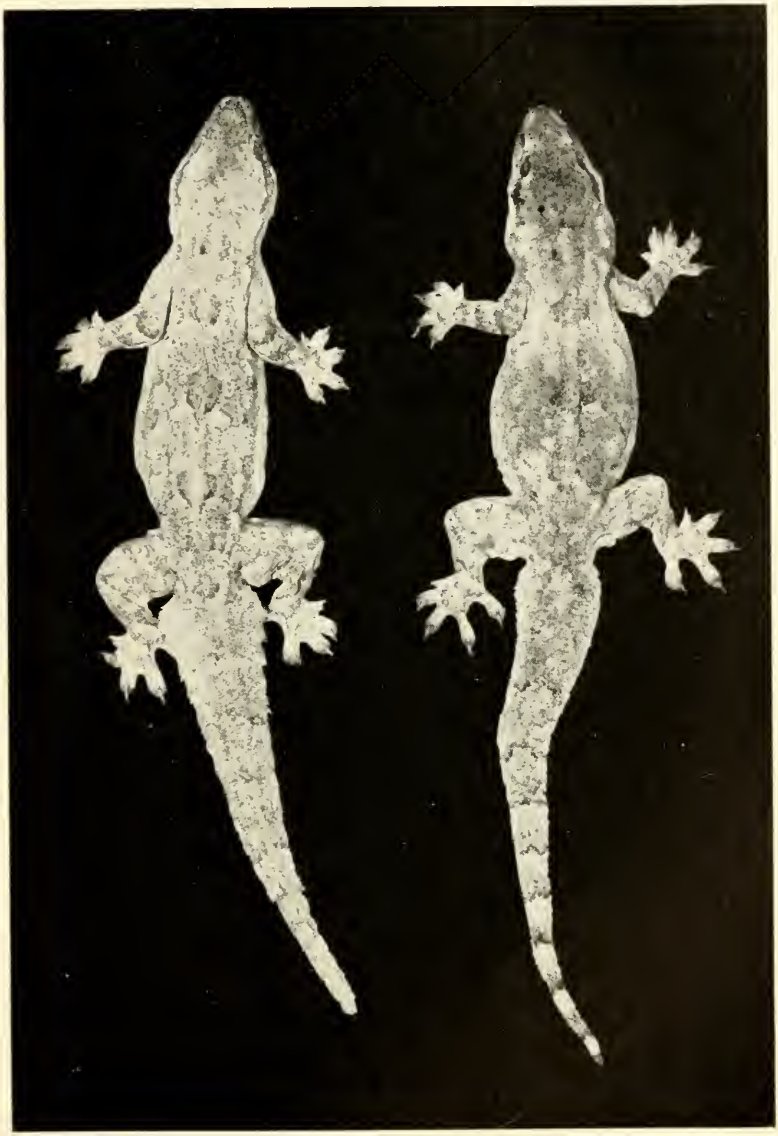


FIG. 17.—*Platyurus platyurus* (Schneider). Left figure, No. 34449 ♂, Pattani, Pattani province Thailand. Actual length, 111 mm. Right figure, No. 33704 ♀, Chiang Mai, Chiang Mai province, Thailand. Actual length, 118 mm.

series of four darker median spots sometimes divided by a light-gray line, the spots tending to connect laterally with an irregular somewhat less dark marking. There are transverse grayish marks on arms and less distinct ones on legs. An indistinct darker band along side of snout, head, and neck, passing above arm to groin. Tail dimly banded with narrow dark-gray and wider light-gray bands indicated on undersurface only on the fringe; chin, venter, and subcaudal region cream with some yellowish wash.

Measurements in mm.: Snout to vent, 57; tail, 63; width of head, 12.4; length of head, 15; snout to arm-insertion, 22.6; axilla to groin, 27; arm, 18; leg, 21.

Variation: The sides of the median dark spots are intensified in some specimens and the series on each side simulates a broken stripe. The top of the head is usually smoky gray. Older specimens have wider, somewhat plumper tails. However, the undersurface of all are flat. The tails are very fragile; about one out of ten has a tail that is complete.

The numbers of femoral pores varies from 32-38, the higher numbers being most frequent. The pores are transversely elongate forming slits across the scales. The series on each side are curved laterally forming a median angle.

Many specimens have large deposits of calcium (otoliths) about the auricular opening.

The color varies, especially in preserved specimens, many appearing cloudy gray with scarcely any pattern indicated.

Distribution: The species is ubiquitous in Thailand, probably the most common house-gekko or *chinchook* in the country.

Outside of Thailand it has been found in Ceylon, India, Sikkim, South China, Malaya, and it occurs widely in the Indo-Australian Archipelago, and the Philippines.

Remarks: This species lays two eggs.

Platyurus craspedotus (Mocquard)

FIG. 18

Hemidactylus craspedotus Mocquard, Le Naturaliste, 1890, p. 144 (type-locality Kina Balu, British North Borneo).

Mimetozoon floweri Boulenger, Proc. Zool. Soc. London, 1896, p. 767 (type-locality, "Crag" Hotel, Penang Hill, 2200 ft., Malaya); A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 46.

P[laturus] craspedotus: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 102.

Diagnosis: Trace of a small dermal fringe on side of head; strong dermal flaps bordering limbs and sides of body; tail with a broad

denticulate fringe; median subcaudals widened; preanofemoral pores, 16-19 on each side separated mesially by several scales.

Description of species (from EHT-HMS No. 3871, Khao Chong Forest Experiment Station, Trang provinces, Thailand): Body and limbs depressed; head scarcely distinct from neck; snout

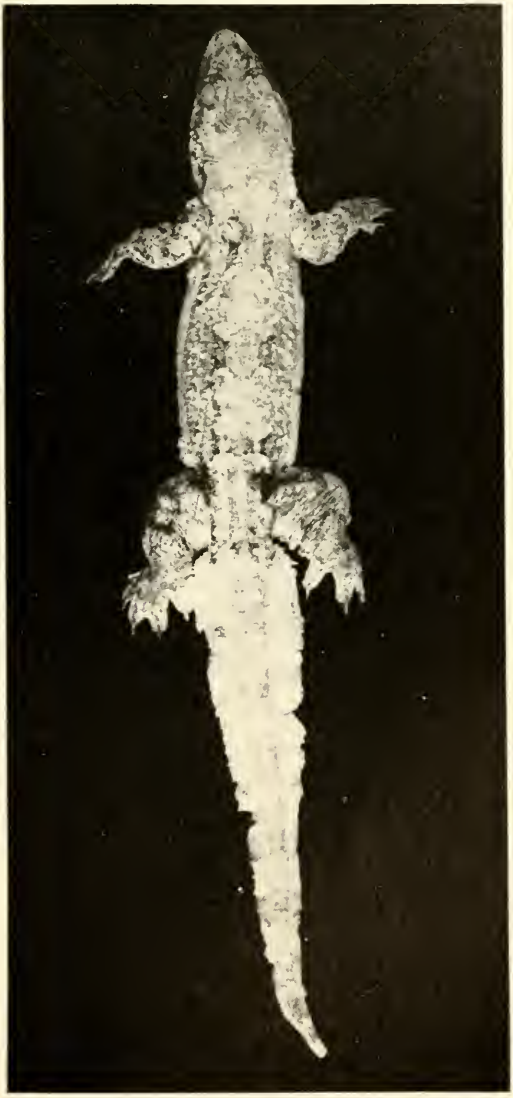


FIG. 18.—*Platyurus craspedotus* (Mocquard). EHT-HMS No. 3871, Khao Chong Forest Experiment Station, Trang province, Thailand. Actual length, 127.5 mm.

obtusely pointed, longer than distance between eye- and ear-opening; rostral two thirds as high as wide, bordered posteriorly by first supralabials and two supranasals; a suture enters rostral from above and continues to a dorsal depression in the scale; nostril surrounded by rostral, supranasal, first labial, and two postnasals, lower the larger; snout pinched-in somewhat behind nostrils; a deep frontal depression more or less connected with the occipital depression; 29 or 30 scales across snout between second supralabials; about 56 scales across snout between fifth supralabials; eleven supralabials, last two small, and beyond these there are minute scales bordering mouth to angle but near these there is a series of five larger scales; eight infralabials, anterior ones very large; mental large triangular; a pair of large median chinshields forming a median suture; second chinshields separated by these but also in contact with infralabials; third chinshields small, separated by seven scales from each other, from infralabials by a single scale.

Snout covered with flat juxtaposed scales a little larger than those in occipital region but practically same as those on dorsum; about 14 irregular rows of enlarged, rounded conical tubercles on dorsum, some extending as far as rostral, those in occipital region smallest; tail showing distinct segments, each basal segment with about 10 rows of transverse scales and with a pair of large flattened tubercles; on sides of tail a dermal fringe edged with numerous denticulate scales larger than dorsal caudals; scales on chin and throat small juxtaposed; ventral surface of body with about 70 rows of scales, those hidden under lateral dermal flaps small, others subcircular, subimbricate; at least those on anterior part of body serrate on posterior edge; in femoral region an elongate series of large scales, each bearing a lunate or oval preanofemoral pore, the series separated by five scales mesially, sixteen on each side; a much-enlarged median series of about 50 subcaudal scales; scales at base small; a lateral denticulate flap on each side of tail; no spines on hemipenial swelling on underside of base of tail.

A lateral skin-fold below horizontal ear-opening; a skin-fold on front and back of arm, and also on leg; digits about two-thirds webbed; all digits with a double row of lamellae; distal phalanges compressed, slender, elevated, arising from widened portion of digit; all digits clawed.

Color: Above generally gray, speckled with paired quadrangular brown spots; a dark line from eye back to elbow; one or two dark longitudinal lines along sides of body; lateral membrane on body

whitish below, brown-spotted above; tail more or less banded posteriorly. Head with indefinite brownish marks; chin, throat, and labials with small brown flecks; venter nearly uniformly white (yellow in life).

Measurements in mm.: Snout to vent, 62; tail, 65.5 (tip regenerated); total length, 127.5; width of tail at base, 11; width of head, 15; length of head, 16.5; snout to arm-insertion, 24; axilla to groin, 28; arm, 19; leg, 22.

Variation: Two other specimens are at hand: B. M. No. 1926. 12.7.7. (6157) from "Foot of Ronpibun Hill, Nakhon Si Thammarat, Thailand; No. 1930.10.9.2. Perak, Malaya. The first has 60 subcaudals, 19-20 preanofemoral pores separated by four scales: scattered tubercles on the frontal and snout areas; greatest width of lateral body fringe 3 mm. The second specimen is a female, and differs in the absence of the preanofemoral pores and while the scales on the snout are a little larger than body-scales the tubercles are absent on snout and occipital region. There are three or four larger scales on the anterior part of the supraocular region and tubercles are present over the dorsum.

In this specimen the mental is a little more elongate, the median chinshields forming a suture for about half their length.

Remarks: The wisdom of maintaining a separate genus for this species, as has been done in the past, is questionable. It agrees with *Platyurus platyurus* in almost if not all general characters. The differences are only differences of degree. Thus the lateral fringe is somewhat wider, the tail fringe wider, the fringe on limbs greater, the webbing between digits greater. There is even a small lateral fold indicated below the ear in *platyurus.* The general characters of the foot are the same. *Platyurus,* however, lacks the enlarged tubercles on dorsum and head.

The two genera were united by Malcolm Smith (1935). In this I concur.

Genus Peropus Wiegmann

Peropus Wiegmann, Nova Acta Acad. Caes. Leop.-Carol., vol. 17, 1835, p. 238 (type of genus, *mutilatus*).

Diagnosis: Digits free, or with a web at base of digits; median part of each widened, with paired lamellae on undersurface preceded by a single lamella. Distal phalanges of four outer digits on hand and foot slender, clawed, free, arising angularly from middle of widened portion; inner digits well developed usually with claw but lacking distal free phalanges; dorsal scales small, granular; sub-

caudals small or widened; pupil vertical; in males preanal and femoral pores present, usually in a continuous series.

There has been much confusion as to the proper generic name for this group of lizards. Stejneger (Proc. U. S. Nat. Mus., vol. 21, 1899, p. 796, and Bull. U. S. Nat. Mus., No. 58, 1907, pp. 180) has shown that the name *Peropus* of Lay and Bennett, for a genus of fishes, was not actually *published* until about 1840 and is antedated by *Peropus* Wiegmann by several years. Unless this can be successfully refuted the name *Peropus* must stand for this genus instead of *Gehyra*.

This species is domestic in habit and has been widely distributed by man. It occurs widely in South Asia, and has reached Australia, Polynesia, and even Mexico.

KEY TO SPECIES OF PEROPUS IN THAILAND

1. Subcaudal region with a median series of large transversely widened scales; dorsal body scales not distinctly conelike; pores variable . . . 2
   Subcaudal region with several series of small scales not transversely widened; ten preanal pores on each side forming a continuous series, angular mesially, extending slightly on to femora . . . *laceratus*
2. Tail much widened behind vent . . . 3
   Maximum width of tail not or but slightly wider than base, scales on dorsum small, flat, cycloid, imbricating, with a slight lateral caudal fringe, not or scarcely denticulate; 15-18 femoral and preanal pores continuous, angular mesially . . . *angusticaudatus*
3. Femoropreanal pores lunate or oval, 15 to 20 on each side forming a doubly-curved, continuous series, angular mesially extending nearly entire length of femora; a pair of rather large supranasals in contact mesially; tail denticulate on sides . . . *mutilatus*
   Femoropreanal pores eleven on each side, small, subcircular forming an angle mesially and reaching about halfway along femora; supranasal smaller, separated mesially; a slight caudal fringe, somewhat denticulate . . . *fehlmanni*

Peropus laceratus Taylor

FIG. 19

Peropus laceratus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp, 218-221, fig. 4 (type-locality, Kanchanaburi, Kanchanaburi province, western Thailand).

Diagnosis: Preanal pores, 20, forming an angular series extending slightly onto femoral region; preanal area covered with enlarged, somewhat pointed scales, but scales on areas lateral to this on underside of femora scarcely half as large. About 48 scales in a line across venter between indistinct ventrolateral folds, scales pointed posteriorly rather than rounded; no web on hand or foot; ten labials to a point below median part of eye; tail distinctly

shorter than body, subcaudals not widened, median five or six rows similar to scales on venter; segmentation of tail not clearly indicated; dorsal scales very small, nearly uniform.

Description of type: Snout oval, with a frontal depression extending back between orbits to a shallow depression on occiput; areas in front of orbits distinctly swollen; rostral one and three-fourths times as wide as high, its median upper portion with a depression and an entrant groove from above; a pair of enlarged supranasals separated mesially by a small scale; nostril bordered by rostral, supranasal, first labial, and three small postnasals; 53 scales across snout at level of suture between fifth and sixth labial; twelve supralabials, tenth, or tenth and eleventh below middle of eye; a series of tiny scales from last supralabial to back of mouth-angle. Mental moderate, its border on mouth equal to that of rostral, forming a right angle with median pair of chinshields, each of which is pointed anteriorly and rounded behind; second pair of chinshields lateral to first, angular anteriorly, rounded behind; third chinshields small, followed by a row of slightly enlarged scales bordering infralabials; ten or eleven infralabials, ninth below eye; last followed by tiny scales to mouth-angle; chinshields somewhat raised and rounded across upper surface, with regular depressions between them; eye moderate; "eyelid" evident from the median lower edge of eye, running around the front and upper edge of eye; length of snout from orbit (5.5 mm.) greater than diameter of orbit (4 mm.).

Arm moderate, with an indistinct narrow web in front of elbow; all digits widened, the shortest with five, longest with seven paired lamellae and a single anterior one; lamellae following on narrow proximal portion of digit scalelike, paired or single (on outer part there may be as many as four rows of scales). From middle of upper surface of widened portion of digits, distal clawed joints arise nearly vertically or bend forward on all digits except inner finger which lacks the terminal phalanges but has a small claw.

Scales of dorsal and lateral surfaces of head and body very small, conelike tubercles varying somewhat in size on head but on body tending to form straight longitudinal and diagonal rows. Scales on venter in about 48 rows between the slight ventrolateral folds; scales imbricate, bluntly pointed, rather than rounded, in fairly straight longitudinal rows. In preanal region larger scales form a somewhat angular series bearing 20 preanal pores and some scales following these bear indistinct depressions; pore-scales followed by four shorter angular series in the region preceding vent; four or

five subcaudal scalerows, larger than adjoining scales but median series not widened transversely, the scales resembling those on venter. Segmentation of tail not or scarcely discernible.

No webs between digits on hand or foot; ear small, situated on a level with lower part of eye; tail thickened, widened near base.

FIG. 19.—*Peropus laceratus* Taylor. Type. From Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, No. 7, fig. no. 4.

Color: Above gray on back and sides, with small, darker gray spots of which there are about twenty on head: spots on body and sides a little larger, more widely scattered, with a double row of very indistinct rounded lighter spots on back; some darker spots on middle of limbs; undersurfaces of body cream to whitish yellow.

Measurements in mm.: Snout to vent, 55; tail, 38; total length, 93; width of head, 12; length of head, 15; tip of snout to arm-insertion, 18; axilla to groin, 25; arm, 17.5; leg, 21.

Variation: No. 33471, a young male topotypic paratype has the pore-scales forming a highly arched angular series, nine on each side, the median one almost separating the two mesial pore-scales that are normally in contact; the dorsal and lateral caudal scales form distinct transverse scalerows ventrally; the segments can be discerned since the last transverse row of subcaudal scales usually has one a little larger than the others.

A second young male (No. 33280 from Ang Hin, Chon Buri) has a similar series of pores but a median scale separates the two series of pore-scales. Another specimen, No. 33281 has lost all skin from the preanal area.

In markings, all are much the same except that the rounded lighter marks may be dimly present over entire dorsal and lateral surfaces of body.

Distribution: Known only from the type locality and Ang Hin, Chon Buri province. All were found under rocks or logs.

Remarks: In the type the widened basal part of the tail contains bony vertebrae; the distal portion (6 mm.) shows two regenerated areas, the last about two millimeters in length.

The skin, as in *Peropus mutilatus*, is extremely fragile, and the skin surface is badly broken. The type, a female, contains two large eggs.

Peropus angusticaudatus sp. nov.

Fig. 20

Type: No. 1035; Siracha, Chon Buri province southeastern Thailand; Edward H. Taylor coll. Apr. 15, 1960.

Paratypes: No. 1033, 1034, 1036, 1037, topotypes, same date and collector.

Diagnosis: Tail distinctly longer than head and body, not or scarcely widening beyond base, much attenuated distally; the hemipenial swellings in males with two small tubercles; edges of tail with a narrow non-denticulated fringe; tail not flattened below but

with a distinct rounded median ridge extending to near tip; male with a series of 15 to 18 large femoropreanal pores on each side.

Description of type: Rostral wider than high with a median straight entrant suture, and bordered on each side by one supralabial, nostril and a supranasal; supranasals quadrangular forming a mutual suture with each other; nostril surrounded by these scales and two small postnasals; a row of slightly larger scales behind supranasals; about 24 scales across snout between posterior edges of second supralabials; about 40 scales between back edge of fourth supralabials; about 33 scalerows between median edges of eyelids; seventh supralabial below middle of pupil followed by three very small supralabials, and a series of about eight granular scales to mouth-angle; mental moderate, as wide as rostral, shape of a quadrant, followed by a pair of chinshields wider anteriorly than posteriorly and flanked on each side by a second pair, narrower and shorter; third pair scarcely differentiated, separated from infralabials by one or two scales; eight or nine infralabials last three small, followed to angle of mouth, by five small granular scales; ear-opening small, its greatest diameter, (1.5 mm.) in diameter of orbit, (3.6 mm.) more than twice; areas immediately posterior to eyes swollen; scales on snout larger than granules of interorbital and occipital areas, or of the shoulder area between arms; body scales subequal, juxtaposed or slightly imbricate, those on sides a little larger than others, rows somewhat irregular; about 35 rows of cycloid, imbricate scales on venter, scales much larger than dorsal scales; scales small on chin, throat, and breast; a doubly curved series of 37 large transversely oval femoropreanal pores angular mesially extending to near distal end of femur; pore-scales preceded by several transverse curving rows of scales, and followed by another; hemipenial swellings relatively small with one or two very small lateral tubercular scales; base of tail relatively narrow, tail not widening suddenly (as in *P. mutilatus*).

Tail slender becoming greatly attenuated, terminating in a very fine tip. Tail not flattened below but with a median rounded slightly elevated ridge; tail somewhat elevated above the borders with a narrow fine nondenticulated fringe.

Fingers short, the outer basal portion widened with five or six lamella below, all divided except terminal; proximal joints with two or three rows of fine undifferentiated scales; a small web, at least between second and third and third and fourth fingers; distal joints arise and stand nearly erect from widened portion of digit on all

except inner finger which lacks distal portion entirely (the fifth finger of right hand is anomalous in also lacking the distal phalanges). I can find no claw on first finger. Toes similar to fingers; fourth and fifth longer than other toes; inner toe lacks distal phalanges but a claw is present. When limbs are adpressed they overlap length of fourth toe.

Color in life: Nearly uniform dark gray above on body, somewhat lighter on head, and darker lavender on tail with a suggestion of lighter bands distally; chin, throat, and venter yellowish-white but

FIG. 20.—*Peropus angusticaudatus* sp. nov. Left figure, Type, No. 1035. Right figure, Paratype, No. 1034. From Siracha, Chon Buri, Thailand.

Table of data on type and paratypes of *P. angusticaudatus*

NUMBER	1036	1037	1035	1033	1034
Sex	♀	♂	♂	♀	♀
Length to vent	57	54	54	51	51
Tail length	47.5*	43*	61.2	53	53
Total length	104.5	97	115.2	104	104
Snout to arm	21	20	19	20	18.5
Axilla to groin	27	26	26	26	26
Width of head	11.8	11.5	10.4	10.1	10
Length of head	15	14.2	14	13	13
Arm	15	15	14.8	15	14.3
Leg	18.3	18	19	17.5	18.2
Pores	0	15–16	18–19	0	0

* Regenerated.

all scales peppered with fine pigment dots; subcaudal area darker, growing nearly blackish towards tip.

Distribution: Known only from Siracha, the type locality, in Chon Buri province.

Remarks: The specimens were taken in an old bamboo-nipa house that was being torn down. Numerous *Hemidactylus frenatus* were taken at the same place.

The regenerated tail is slightly denticulated, more flattened ventrally the subcaudals are wider, than in *mutilatus* and the dorsal caudal scales are not in straight transverse rows.

Two other species of *Peropus* are known in Chon Buri province: *P. laceratus* and *P. mutilatus*.

Peropus fehlmanni Taylor

Peropus fehlmanni Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 221-224, fig. 5 (type-locality, 4 Km NW Kanchanaburi Kanchanaburi province, western Thailand).

Diagnosis: Scales on dorsal part of head and body not distinctly conical; scales on snout subimbricate, double size of those on occipnt and interorbital region; small distinct webs between digits on hands and feet; subcaudal scales at base of tail somewhat enlarged, followed by a single row of greatly enlarged subcaudals; largest body scales in preanal area; femoropreanal pores 22 forming an arched series extending onto femur for nearly half its length; scales on dorsal surface of slender tail somewhat irregular not forming distinct transverse rows; segments of tail not or scarcely indicated; seventh or eighth supralabial, and seventh infralabial below pupil of eye; third (outer) pair of chinshields separated from infralabials; ventrolateral fold not indicated.

Description of type: Rostral twice as wide as high, with a slight median depression on upper border and with an entrant suture whose length is slightly less than half height of scale; nostril surrounded by rostral, first supralabial, a supranasal, and two clearly differentiated postnasals; a slight frontal depression; supranasals separated by two small scales one behind the other; about 44 scales across snout between fifth supralabials; eight supralabials, last two small, with a row of about ten small body scales to mouth-angle;

FIG. 21.—*Peropus fehlmanni* Taylor. Type. From Taylor, Univ. Kansas Sci. Bull., vol. 43, No. 7, 1962, fig. 5.

seven infralabials, likewise followed by small scales to mouth-angle; mental with labial border equal to that of rostral, shaped like a quadrant; length of snout (4.2 mm.) greater than diameter of orbit (3.5 mm.); ear rather large (.7 to 1.0 mm. in diameter); median pair of chinshields pointed (angular) anteriorly, the width across upper half much greater than width posteriorly; second pair of chinshields much smaller than first, separated by first pair; third pair separated by preceding pairs and separated from infralabials by a scale; lower edges of chinshields forming a curve.

Arm with a very slight web in front of elbow joint; a distinct but small web between fingers; digits widened, each bearing six or seven paired lamellae preceded by a single lamella on under surface of widened part. Toes, similarly widened, one-fourth webbed. On all digits except inner, two distal phalanges rise vertically from near middle of upper surface of widened part, all clawed; inner digits lack two distal phalanges, but a small claw present at anterior edge of widened portion.

Scales on snout irregularly shaped, distinctly not conical, in places subimbricate. Scales on sides and latter half of back juxtaposed, flat, and much larger than scales on shoulders, neck, or occiput; venter covered with somewhat larger imbricating scales in about 42 rows; those low on sides and those on sides of venter not or scarcely differentiated from each other; seemingly there are no ventrolateral folds. An angular series of small rounded femoropreanal pores, eleven on each side extending halfway on femora.

Scales on dorsal and lateral surface of tail irregular, suggesting the possibility that the entire tail has been regenerated; tail narrow with a slight fringe along edges and tapering rapidly to a fine point; subcaudal scales widened, appearing to be normal and not reproduced.

Color: Above light-brown with black flecks scattered on head, body, limbs, and tail; ventral surface yellowish white, but all scales with small pigment dots; underside of tail more heavily pigmented with brown; the pigment on pore-scales tend to make an indefinite brownish circle on scale, but is not especially conspicuous.

Measurements in mm.: Snout to vent, 37; tail, 33; total length, 70; width of head, 8.2; length of head, 11.8; snout to arm-insertion, 15; axilla to groin, 16; arm, 10.5; leg, 13.2.

Variation: Not known.

Distribution: Known only from the type locality and Ronpibon, Nakhon Si Thammarat.

Remarks: The specimen was taken at night along the edges of a small rain-pool close to the road. It was moving about on the ground when discovered.

The second specimen in the collection, No. 35526 ♀, is from near Tonka Harbor Tin Mine, Ronpibon, Nakhon Si Thammarat. It has a snout-to-vent length of 40 mm. There is a rather sharply defined canthal line of cream dots bordered below by a darker line passing through the eye and terminating on the side of the neck. Two dark-brown marks extend back from nostrils to the frontal region; the back is brownish with small darker brown spots, some arranged transversely and at least two indefinite longitudinal rows of white dots or flecks. The ventral surface has a dense powdering of cinnamon-brown. The tail has been lost.

Peropus mutilatus (Wiegmann)

Fig. 22

Hemidactylus (Peropus) mutilatus Wiegmann, Nova Acta Acad. Caes. Leopoldino-Carolinae . . ., vol. 17, 1835 (type-locality, Manila, P. I.).

Hemidactylus mutilatus: Duméril and Bibron, Erpétologie générale . . ., vol. 3, 1836, pp. 354-355.

Peropus mutilatus: Fitzinger, Systema Reptilium, 1843, p. 103.

Dactyloperus insulensis: Girard, U. S. Exploring Expedition . . . Herpetology, 1858, pp. 277, 280 (type-locality, "Sandwich Islands"-Hawaiian Islands).

Hemidactylus (Peripia) mutilatus: Peters, Monatsb. Akad. Wiss. Berlin, 1867, p. 14.

Gehyra mutilata: Boulenger, Catalogue of the lizards in the British Museum (Natural History), 2nd Ed., vol. 1, 1885, pp. 148-149; The fauna of British India . . . Reptilia and Batrachia, 1890, pp. 96-97, fig. 28 (foot); Flower, Proc. Zool. Soc. London, Dec. 1, 1896, pp. 866-867; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 47; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, p. 152 ("Bangnara, Patani"); *ibid.*, vol. 2, June 1916, p. 52.

Peropus mutilatus: Stejneger, Proc. U. S. Nat. Mus., vol. 21, 1899, pp. 796-798, fig. 5 (chin); Bull. U. S. Nat. Mus., no. 58, 1907, pp. 180-182, figs. 171-173; Barbour, Mem. Mus. Comp. Zool. Harvard Col., vol. 44, 1912, 81; Taylor, Philippine Journ. Sci., section D, vol. 12, 1917, pp. 368-369; Dept. Agri. Nat. Res. Bureau of Sci., publ. No. 17, Dec. 12, 1922, pp. 62-65, fig. 6; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, p. 1082 (Loei, Rat Buri, and Nakhon Ratchasima, provinces).

Hemidactylus peronii Duméril and Bibron, Erpétologie Générale . . ., vol. 3, 1836, p. 352, pl. 30, fig. 1 (type-locality, l'Ile-de-France = Mauritius).

Peripia peronii: Stoliczka, Journ. Asiat. Soc. Bengal, 1870, p. 163; Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Cambodge, 1885, pp. 86, 103.

Dactyloperus insulensis Girard, Proc. Acad. Nat. Sci. Philadelphia, 1857, p. 197 (extra p. 5) (type-locality, Hawaiian Islands).

Hemidactylus platyurus Bleeker, Naturrk. Tydschr. Nederland Ind., vol. 16, 1858, p. 31 (type-locality, Java, Sumatra, Nias, and Banka).

Gecko pardus Tytler, Journ. Asiat. Soc. Bengal, vol. 33, pt. 2, 1864, p. 47. (Type-locality ?.)

Peropus packardii Cope, Proc. Acad. Nat. Sci. Philadelphia, 1868, p. 319 (type-locality, Penang, Malaya).

Hemidactylus navarri Dugès, La Naturaliza, vol. 6, 1883, pp. 309-312, pl. 7 (type-locality, San Blas, Nayarit, Mexico).

Gehyra beebei Annandale, Rec. Ind. Mus., vol. 9, 1913, p. 307 (type-locality, Sarawak, Borneo).

Diagnosis: Scales following the widened divided lamellae on underside of digits, small in two or more rows; digits with very small webs between fingers, larger ones between toes; two or three pairs of chinshields; a long continuous series of from 25 to 41 lunate femoropreanal pores, angular mesially; rather large supranasals in contact with each other mesially. Tail depressed, usually flat on undersurface, laterally more or less denticulate. Skin fragile.

Description of species (from No. 76): Rostral (2.7 mm.) wider than high (1.5 mm.); somewhat flattened and depressed above with an entrant suture from above; a pair of enlarged supranasals in contact mesially; nostril surrounded by rostral, first supralabial, supranasal and two postnasals; a small frontal depression, area in front of orbits swollen; about 44 scales across snout between sutures of fourth and fifth supralabials; eight or nine supralabials, last two very small followed by eight to ten granules to mouth angle; eye moderately large its diameter (3.6 mm.) much less than length of snout (5.3 mm.); ear-opening with a diameter of .72 millimeters; infralabials seven, last small, followed by a row of granular scales to angle of mouth; mental with a labial border distinctly less than that of rostral; median pair of chinshields angular anteriorly, scales wider anteriorly than posteriorly; second pair of chinshields separated by first pair; third pair broken up into small scales, scarcely distinguishable as chinshields.

Arms short, digits dilated proximally with a series of lamella below, first single, next six paired, followed behind by two or three rows of small scales; two distal phalanges compressed, clawed, arising from middle of widened area except on inner finger which has a claw but no distal phalanges; legs short, adpressed limbs overlapping length of longest toe; a small web-remnant between digits; seven paired lamellae under longest toes, the scales in several rows under proximal part of toes. Tail broadened, nearly flat on ventral surface, the median scale series widened; tail segmented, the segments indicated by slightly larger denticulations.

Scales on snout somewhat irregular larger than those on occiput, but smaller than those on sides of body; scales not or scarcely im-

FIG. 22.—*Peropus mutilatus* (Wiegmann). EHT-HMS No. 76 "Thailand." Actual total length, 120 mm.

bricate the scales usually somewhat elevated frequently touching adjoining scales at only one or two points; a vague ventrolateral fold; scales behind chinshields on throat small, imbricate; scales on venter in about 38 rows, oval, rather than cycloid, imbricating, distinctly larger than dorsal scales for the most part. Scales in region below femora in regular curving transverse series; a series of transversely elongated femoropreanal pores, 13-18 (the irregularity partly due to a small injury), forming a median angle, and curving on each side. This series followed by one complete row of scales equally as large as the pore-scales. Tail segmented, basal segments with from ten to eleven nearly straight rows of small imbricating scales; median subcaudals much enlarged and widened, two to each segment; distal part of tail regenerated. No distinctive spines at base of tail.

Color: Dorsal surface brownish lavender nearly uniform with two median rows of dim rounded light spots; underside of head, venter and subcaudal region nearly yellowish white with a microscopic peppering of dark pigment; side of head lighter than dorsum.

Measurements in mm.: Length, snout to vent, 58; tail, 61; snout to arm-insertion, 19.5; axilla to groin, 26; width of head, 12.5; length of head, 15; width of tail near base, 10.8; arm, 16; leg, 19.

Variation: The femoropreanal pore-series varies ordinarily from 17-22 on each side and only rarely are they separated mesially. The thickness of the tail varies somewhat with age, the older specimens usually having a plumper tail.

Distribution: This species is very widely spread in Thailand, probably occurring in all provinces in suitable localities. It is equally common in houses in towns, villages and cities, as it is in the forest.

Outside of Thailand the species is in India, Ceylon, Burma, southern China, Indo-China, Malaya, the Indo-Australian Archipelago to the Philippines and Oceania; Mexico.

It is most likely that man has played an important role in distributing this species, either by accidentally transporting the animal or its eggs in baggage; or by specimens living on boats, leaving their home later to disembark in foreign ports.

Hemiphyllodactylus Bleeker

Hemiphyllodactylus Bleeker, Nat. Tijdschr. Ned.-Indie, vol. 20, 1860, p. 327 (type of genus *Hemiphyllodactylus typus*); Stejneger, Proc. U. S. Nat. Mus., vol. 21, 1899, p. 799; Brongersma, Zool. Meded., Leiden, vol. 15, 1932, pp. 211-213.

Spathodactylus Günther, Proc. Zool. Soc. London, 1872, p. 594 (type of genus *Spathodactylus mutilatus*).

Spathoscalabotes Boulenger, Catalogue of the lizards in the British Museum (Natural History), 2nd Ed., vol. 1, 1885, p. 157 (substitute name for *Spathodactylus* (*non*-Pictet) Günther).

Lepidodactylus (*part.*) Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 162.

Diagnosis: Four outer digits clawed, well developed, inner digit vestigial, not webbed, with or without claw, cylindrical at the base; digits bearing widened lamellae, at least distal ones divided mesially by a groove; last joints of digits short, arising from within widened part of digit (absent on inner digit). Dorsal scales small, granular, lacking enlarged tubercles; ventral scales cycloid, likewise small; preanal and femoral pores present; pupil vertical.

This genus of diminutive geckoes has suffered from synonymyzing and a revision of the group will undoubtedly show that certain synonymized forms well merit specific designation. Malcolm Smith states the matter as follows: "In a form so widely distributed it is only to be expected that small morphological differences such as the number of labials, the size of the postmental shields and of the digital expansions and the number of preanal and femoral pores should be found." Often "small morphological differences" seen in a diminutive gecko are judged insignificant, but the same seen in a gecko of considerably greater size, would most certainly be regarded as significant.

Two species are recognized in this paper; one that has been called *Hemiphyllodactylus typus;* the other a species recently acquired from Phu Kading by Mr. Kumpol Isarankuara, Curator of the Zoological Collection of Chulalongkorn University. This I am referring to *H. yunnanensis.*

The two forms may be distinguished by the following key:

KEY TO THAI SPECIES OF HEMIPHYLLODACTYLUS

Hind limb not reaching to more than half way between the axilla and groin; no distinct postmentals; males with preanal and femoral pores, *typus*

Hind limb reaching more than half way between axilla and groin; postmentals distinct, males with preanofemoral pores in a singles series ..... *yunnanensis*

Hemiphyllodactylus typus Bleeker

FIG. 23

Hemiphyllodactylus typus Bleeker, Nat. Tijds. Nederl.—Ind., vol. 20, 1860, p. 327 (type-locality, Gunong Paring, Java); De Rooij, The Reptiles of the Indo-Australian Archipelago, vol. 1, Lacertilia, Chelonia, Emydosauria 1915, pp. 46-47, figs. 29, 30; Boulenger, Ann. Mag. Nat. Hist., ser. 5, vol. 20, 1887, p. 152; Brongersma, Zool. Med. Leiden, vol. 15, 1932, pp. 211-217 (monographic treatment, with bibliography); Deraniyagala, Ceylon Journ. Sci., sec. B, vol. 16, 1932, p. 308; M. Smith, Rec. Ind. Mus., vol. 35, 1933, p. 16.

Lepidodactylus ceylonensis Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885; p. 164, pl. 13, fig. 3 (type-locality, Gampola, Ceylon); The fauna of British India; Reptilia and Batrachia, 1890, p. 98; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 316; Annandale, Journ. and Proc. Asiat. Soc. Bengal, n. ser., vol. 1, 1915, p. 84; Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, 1915, p. 239.

Spathodactylus mutilatus Günther, Proc. Zool. Soc. London, 1872, p. 594 (type-locality, Agam, Sumatra).

Spathoscalabotes mutilatus: Boulenger, Catalogue of the lizards in the British Mus., vol. 1, 1885, p. 157, pl. 13, fig. 1.

Diagnosis: Transverse lamellae under dilated digits divided mesially; digits either with rudiment of web or entirely free; compressed distal part of digits short, compressed, rising from extremity of dilated part; no claw on inner digit which varies in size; no enlarged tubercles among granular scales on body; ventral scales imbricate, flat. Males with preanal, or preanal and femoral pores.

Description of species (from M 32, EHT-HMS coll. Fraser's Hill, Malaya): Head length (13 mm.) greater than width (9 mm.); rostral more than twice as wide as high (2.3 x 1.1 mm.), bordered by first labial, nostril, supranasal and three small postrostrals; a slight notch above, but no entering suture; nostril surrounded by rostral, first labial, supranasal, and two postnasals; supranasals separated from each other by three rows of scales; 23 scales across snout between suture of first and second supralabials, 42 between fourth labials; supralabials 10-10, first large; seventh directly below pupil of eye; scales on snout and above eyelids larger than those on occiput; scales on shoulders and front part of dorsum smaller than on sides and rump; scales tubercular nonimbricating. Mental triangular, its border on mouth much smaller than rostral border; infralabials, 10-11; posterior labials small; a pair of small median chinshields touch mental; two rows of smaller scales behind chinshields; scales on chin and throat tubercular; scales on breast and venter larger, subcircular, imbricating, gradually merging into small granular scales on side; preanal and femoral pores continuous, angular mesially; area in front of preanal pores swollen (glandular?); scales behind pores very small except in preanal region where there are six or seven arched rows of larger scales; two strong hemipenial swellings each with three large bluntly pointed tubercles near edge of vent; when arm and leg are adpressed the fingers overlap; fingers with widened lamellae beneath, distal ones divided mesially, proximal ones single; four outer toes with distal phalanges compressed, arising from near edge of widened part, each with a claw.

Lamellae: 1st finger, five or six lamellae, none divided, claw absent; 2nd, eight lamellae, two outer divided with one distal

FIG. 23. — *Hemiphyllodactylus typus* Bleeker. EHT-HMS No. 32, Fraser's Hill, Malaya. Actual length, 86 mm.

median undivided; 3rd, ten lamellae, four divided distally with median distal single; 4th, eight lamellae, three outer divided and outermost single. On toes inner has five lamellae, the penultimate divided and with claw; on outer toes, two or three divided lamellae, terminal one small, single, a few proximal ones usually broken into three smaller scales.

A distinct basal web between fingers and toes. Scales on tail forming rather regular transverse rows on dorsal and lateral surfaces; scales on ventral surface larger, three median rows larger than others. The segments are not or very indistinctly marked.

Color: Above gray with a very fine powdering of cinnamon-brown; head rather more yellowish-brown; a dim dorsolateral row of rounded whitish spots from eye to groin. Venter yellowish white.

Measurements in mm.: Snout to vent, 46; tail, 40; width of head, 9; length of head, 13; snout to arm, 17; axilla to groin, 22; arm, 13; leg, 14.

Hemiphyllodactylus yunnanensis (Boulenger)

FIG. 24

Gehyra yunnanensis Boulenger, Ann. Mag. Nat. Hist., ser. 7, vol. 12, 1903, p. 429 (type-locality, Yunnan-Fu).

Cainodactylus yunnanensis: Barbour, Occ. Papers Boston Soc. Nat. Hist., vol. 5, 1924, p. 134, fig. (foot); Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 479.

Hemiphyllodactylus yunnanensis: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, London, Feb. 7, 1930 (Yunnan, N. Laos, Upper Burma).

Diagnosis: A pair of somewhat enlarged postmentals; nine supralabials, ten infralabials; rostral nearly rectangular, with an entrant notch in its upper edge; preanofemoral pores, 12-12 (11-12), transversely widened; subcaudals not strongly widened.

Description of species (from C. U. No. 2676 Phu Kading, Loei province, Thailand): Rostral subrectangular with a small median notch on upper edge; a small pair of supranasals, separated by three granular scales, touching rostral; nostril bordered by rostral, first supralabial, internasal, and two small postnasals; scales on snout and in frontal area larger than those on occiput; occipital granules less than half size of those on frontal area; scales on dorsum larger than occipitals but smaller than scales on snout, cycloid, juxtaposed, becoming somewhat imbricate laterally; ventral scales cycloid, imbricating, the larger more median series double size of dorsal scales; nine supralabials, first largest, last two very small; ten infralabials,

first largest, last three small; pupil vertical; ear small situated below lateral dark neck-stripe, its diameter about one fourth of that of eye; four lamellae under widened part of fourth toe, at least three divided, followed by five or six single oblique scales or lamellae; first finger small with a minute claw, but no elevated terminal joint;

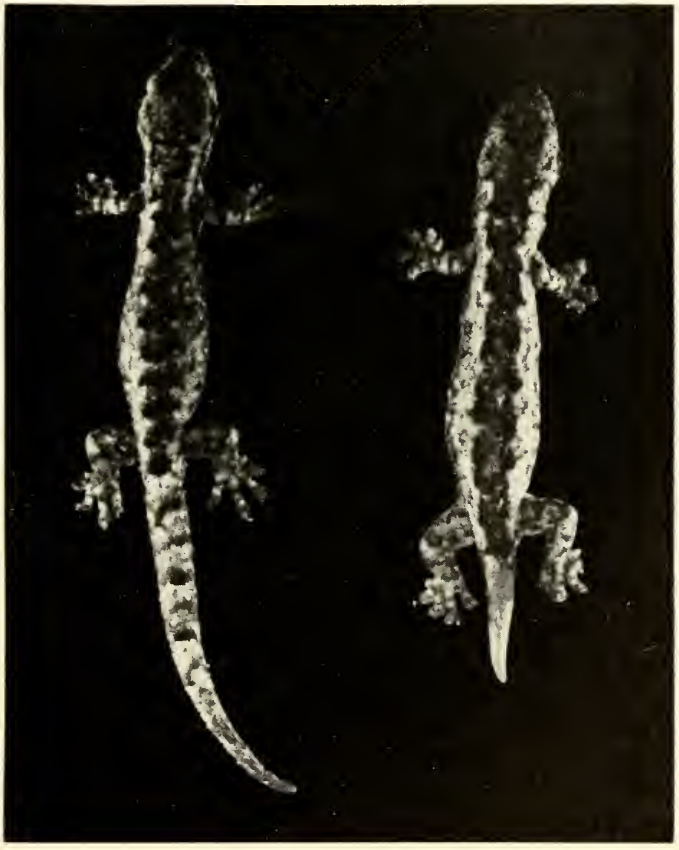


FIG. 24.—*Hemiphyllodactylus yunnanensis* (Boulenger). Left figure, No. 2677, Phu Kading, Loei province, 4800 ft. +. Actual total length, 64 mm. Right figare, No. 2677a, same locality. Actual length, 48 mm.

slight fringe on back of thigh; preanal and femoral pores in a continuous series of twelve (eleven) transversely widened pores, angular medially and extending nearly to knee; a strong tubercle on each side of basal subcaudal (hemipenial) swelling. Scales on dorsum smaller than those on dorsal caudal region; latter scales arranged in straight transverse rows; segments not distinctly marked; lateral

caudal scales considerably larger than dorsal caudals, but smaller than the somewhat irregular subcaudal scales which do not form a much widened median series.

Color: Above two lateral gray stripes with indefinite edges beginning on snout, becoming wider on body; a median darker brown irregular stripe with dark transverse marks on each side of this; (about nine or ten on body); arms and legs mottled brown and black; tail banded black and grayish brown; two indistinct cream spots above on base of tail; top of head variegated brown with some black; a more or less distinct series of cream spots on sides of the brown stripe on middle of back. A dark stripe from tip of snout through eye to above arm with cream-dots on black coloring on side of neck; lower sides flecked or mottled dimly in black or gray-black; underside light cream, finely pigmented; tail on male orange below, the dark bands widening on ventral surface.

Measurements in mm.: Total length, 64; tail (tip regenerated), 26.5; axilla to groin, 18; tip of snout to arm-insertion, 12.8; arm, 7.2; leg, 10; width of head, 6.6; length of head, 9.

Variation: Supralabials vary from 10 to 12; infralabials vary from 9 to 11. There may be one or two pairs of postmentals, the inner ones always the largest. The preanofemoral scales are in a continuous angular series varying from 12 to 22 in number (*fide* M. Smith). The maximum known snout-to-vent length is 42 mm., the total length 78 mm.

This species is very different from *Hemiphyllodactylus larutensis*, its closest geographical relative. A presumed hiatus in distribution of more than 600 miles occurs between the ranges of the two species.

Distribution: This is the first and only record of this species in Thailand. Three specimens were obtained on Phu Kading, Loei province by Nai Kumpol Isarankura of Chulalongkorn University, Curator of University collections.

I failed to find this species while collecting in this locality.

The species is known also in upper Burma, northern Laos, and Yunnan, China.

Genus GEKKO Laurenti

Gekko Laurenti, Specimen medicum, exhibens synopsin reptilium . . . 1768, p. 43 (type of genus, *Gekko verticillatus* = *Gekko gecko Linnaeus*).

Diagnosis: Digits widened, bearing undivided transverse lamellae, with or without webbing; claws present on four outer digits of hand and foot; terminal joint lying above widened portion and

attached to it; inner digit well developed, lacking claw and not extending beyond terminal edge of widened lamellae. Body with minute subequal scales or these with irregular rows of enlarged tubercles. Preanal, or preanal and femoral pores present.

The large *Gekko gecko* has become a very domestic animal and many houses in the city of Bangkok have their quota of individuals. Their presence is made known by their loud call repeated several times. They feed on insects and often consume individuals of the smaller species of domestic geckoes.

Two eggs are laid, usually in a fairly dark place. These are plastered against a surface, the eggs having a flattened biscuitlike shape. Several individuals may lay their eggs close together.

Key to Species of Gekko in Thailand

1. Rostral forming part of border of nostril 2
   Rostral excluded from nostril 3
2. Nine or ten preanal pores; no femoral pores. Gray (yellow in life) with a median and two longitudinal rows of small circular whitish spots alternating with small blackish spots which may be absent ..... *petricolus*
   Sixteen to twenty femoropreanal pores on each side; light brown to fawn, usually with median series of paired blackish spots, *monarchus*
3. Eight to twelve preanal pores on each side forming a continuous series angular mesially; five or six transverse scalerows in each caudal segment; three to five small scales between dorsal tubercles; bluish gray above, profusely spotted with orange-red and grayish white, *gecko gecko*
   Five to eight preanal pores on each side; ten to twelve transverse scalerows on each basal caudal segment; five to eight small scales between dorsal tubercles; gray or bluish gray above with or without indefinite darker spots ..... *smithi*

Gekko petricolus Taylor

Figs. 25, 26

Gekko petricolus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 227-229, fig. 7 (type-locality, Forestry Station, Sanoi River, Ubon province, Thailand).

Diagnosis: None or only merest remnant of a web between digits; inner digits well developed, lacking claws, subdigital lamellae undivided; body covered with fine subequal granules, intermixed with somewhat enlarged tubercles forming irregular rows separated by from two to five granules; postnasal and frontal areas depressed; rostral entering nostril; venter with about 30 rows of larger cycloid scales, somewhat imbricate; subcaudals widened except at base of tail and at tip; each proximal caudal segment with four enlarged

tubercles. Tail slender, depressed; nine or ten preanal pores, no femoral pores. Adults yellow in life with a lavender-gray head; numerous rounded whitish spots evident.

Description of species: Male type. Rostral a little less than twice as wide as high, its upper edge somewhat concave with a Y-shaped median groove; a pair of large supranasals narrowly in contact mesially; nostril surrounded by rostral, supranasal, two postnasals and first supralabial; supralabials twelve, followed by a number of small scales running back to mouth angle; mental with a labial border equal to that of rostral; ten or eleven infralabials, followed by small scales bordering mouth to its posterior angle; mental followed by two somewhat elongate chinshields; these flanked on each side by three (or four) somewhat enlarged chinshields in contact with infralabials; this enlarged series continues back on each side for several scales, but these scales are separated from infralabials by one or more series of small scales; scales on chin and throat small, cycloid, imbricating, their posterior edges serrate or tuberculate when seen under a lens; an occipital depression somewhat separated by a ridge from fronto-interorbital depression; area behind nostril somewhat depressed; about 47 scales across snout between seventh labials; eye large, diameter of orbit (7 mm.), much shorter than snout (10.5 mm.); "eyelid" completely surrounding eye, with a short series of spinous scales on its posterior border; ear-opening moderate, its greatest (diagonal) diameter about three millimeters; largest scales are on snout on an area anterior to eye, and on supraorbital region; interorbital and occipital areas with smallest scales; about 38 scales across head between median edges of upper eyelids. Dorsal scales small, rather uniform, granular, with about 16 irregular rows of larger rounded moundlike tubercles; tail indistinctly segmented, each segment with ten to twelve transverse rows of small scales and with two or more enlarged flattened scales near posterior part of segment; scales of basal subcaudal region not greatly enlarged; transversely widened median plates under tail for most of its length, extending to near tip of tail, where widened scales are replaced by rows of small scales. Tail flattened, narrowed, tapering to a fine point.

Arms and legs well developed; digits with scarcely a trace of webs; divided lamellae under digits except at base; elevated terminal joint with claw, extending beyond widened part of digit; claw absent on inner finger, which otherwise is well developed. About 20 lamellae under fourth finger and toe, basal ones broken or divided into small scales; hind leg reaches beyond elbow; a

FIG. 25.—*Gekko petricolus* Taylor. From Taylor. Univ. Kansas Sci. Bull., vol. 43, No. 7, 1962, fig. 7.

somewhat curved series of nine preanal pores, followed by a preanal area covered by seven rows of widened scales; openings of postanal sacs evident just preceding hemipenial swellings.

Color in life: On back, sides of body, and tail, yellow with small rather symmetrical yellowish-white marks; some darker flecking visible; head lavender-gray; underside of body and tail yellowish to dirty white. In preservative dull gray, white spots rather dimly visible.

Measurements of type in mm.: Snout to vent, 98; tail, 114; axilla to groin, 45; head width, 20; head length, 25.

Variation: The type series, all taken in the same locality, was constant in color save that younger specimens failed to show the yellow coloration but were gray and white in color. The femoral pores were either nine or ten in number, the exudate from them being glass-clear and projecting strongly from the pores. Variation in number of scales across snout between seventh labials is from 43 to 47; across the middle part of venter between the ventrolateral folds, the number of scales varies between 27 and 32.

Sometimes the supranasals are separated from each other by a single scale instead of two scales. The rostral suture in one specimen is X-shaped.

The subcaudal scale-count from vent to tip of tail varies from about 104 to 110, the basal and terminal ones not enlarged.

The color of the adults varies but little. The yellow color disappears in the fixative within 36 hours. One young specimen differs as follows: above generally gray; head somewhat darker with numerous very small blue-white flecks or spots with slightly larger ones on occiput; a few blacker flecks also present; dorsum lighter gray than head with a row of seven small dashlike black marks along the middle line, these marks alternating with rounded bluish-white spots which continue onto tail; a similar dorsolateral and a lateral row of more indefinite dark spots also interspersed with rounded blue-white spots. Arms and legs gray with numerous whitish flecks and spots sometimes tending to form a reticulum; tail light with twelve broad dark-gray bands reaching to ventral surface; entire undersurface of head and body white or cream-white with some yellowish wash; under a lens some scattered fine pigment can be seen, the pigmentation a little heavier under tail. (Specimen figured.)

FIG. 26.—*Gekko petricolus* Taylor. Paratype, young. No. 34853 Forest Station, Sanoi River, Ubon province. Actual length, 136.

Distribution: Known only from the sandstone hills near the border of Thailand and Laos. It probably occurs also in the mountains between Cambodia and Thailand.

Remarks: The weathering of the sandstone exposed along the Laos border leaves boulders and table-rocks in profusion. The animals occupy horizontal crevices between the rocks, in which places they were almost invariably found upside down. Eggs are usually placed on ceilings. In certain small overhanging rocks, remnants of dozens of eggs could be seen on ceilings six or eight feet above the floor. One exception was a pair of eggs placed on a large boulder that offered no crevices. These were on a vertical side of the boulder a few inches from the earth, covered accidentally by a pile of windblown leaves.

The eggs are rather small in diameter (9-11 mm.) and about 8 mm. high. They are somewhat moundlike, the two cemented together and plastered against rock. It is practically impossible to remove them without breaking them.

A single young specimen, No. 34855, was taken at the type locality in 1958. It was found in a pile of discarded boards not far from a group of boulders. Two of the present series were taken in a shelter-house built over exposed boulders at the very edge of the Sanoi River.

At no time did I hear them call.

One pair of embryos taken from eggs, measured 45 mm. (22 mm. snout to vent, the tail, 23 mm.).

Gekko monarchus Schlegel, in Duméril and Bibron

FIG. 27

Platydactylus monarchus Schlegel, in Duméril and Bibron, Erpétologie Générale . . ., vol. 3, 1836, p. 335 (type-locality, Amboyna); Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 625; Girard, United States Exploring Expedition during the years 1838-42, vol. 20, Herp. 1858, p. 292.

Platydactylus (Scelotretus) monarchus: Fitzinger, Systema Reptilium, 1843, p. 101.

Gekko monarchus: Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 16; Günther, Reptiles of British India, 1864, p. 103; Theobald, Descriptive catalogue of the reptiles of British India, 1876, p. 72; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 187; The fauna of British India, . . . Reptilia and Batrachia, 1890, p. 103; Flower, Proc. Zool. Soc. London, 1899, p. 635; Boulenger, Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 150; Boulenger, The vertebrate fauna of the Malay Peninsula, . . . Reptilia and Batrachia, 1912, pp. 51-52; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, p. 152. "Bangnara Patani" [= Narathiwat, Narathiwat]; Bull. Raffles Mus., no. 3, Apr. 1930, p. 18.

Diagnosis: A medium-sized species reaching a snout-vent length of about 100 mm. Digits moderately dilated with a web-rudiment;

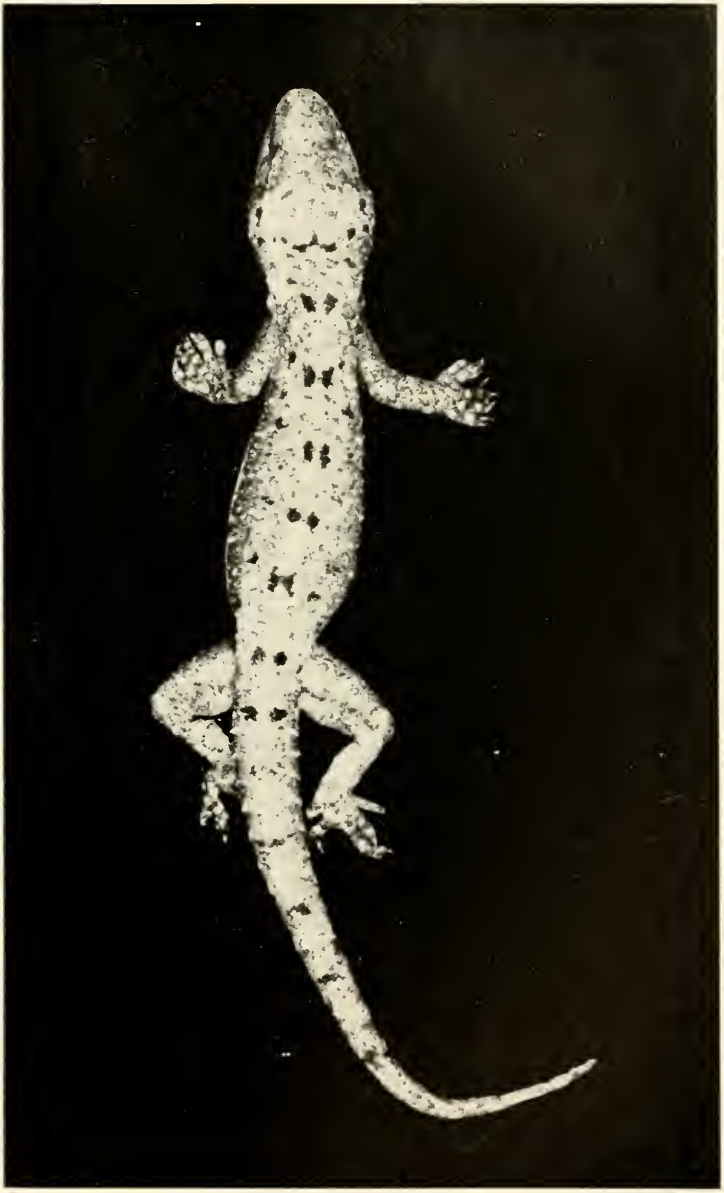


FIG. 27.—*Gekko monarchus* Schlegel, in Duméril and Bibron. EHT-HMS, No. 3355, Maxwell's Hill, Malaya. Total length, 139 mm.

rostral entering nostril; a large median pair of chinshields; back covered with small granules intermixed with larger granules; a long continuous series of preanal and femoral pores, 16-20 on each side. Light brown to fawn with small, usually irregularly paired black spots on head, body, and base of tail; distal parts of tail banded.

Description of species (from No. 30313 from Kuala Lumpur, Malaya): Rostral bordering nostril two thirds as high as wide, notched on median upper edge, with two short grooves or sutures in upper part of scale; nostril bordered by a supranasal, two postnasals, first labial and rostral; a somewhat enlarged scale in rostral notch, followed by two smaller scales, the three lying between supranasals; an occipital depression preceded by an interorbital depression; about 45 scales across snout between sixth supralabials; about 43 granular scales between supraciliary edges across interorbital region; eye rather large, diameter of orbit a little less than half length of snout; scales on snout much larger than those in interorbital region or occiput; eleven distinctly enlarged supralabials, ninth and tenth lying below pupil of eye; width of mental about two thirds of the width of rostral; 12 infralabials, the first largest with a posterior projection; a pair of elongate median chinshields with a smaller outer pair; eight scales lying behind chinshields in a row between third infralabials; ear-opening moderate; scales of dorsum and sides fine, granular, with 16 or 17 irregular rows of enlarged conical or pyramidal granules, smaller mesially and on lower part of sides; venter covered with cycloid imbricate scales between two somewhat indistinct ventrolateral folds, median scales larger than outer; a continuous series of femoropreanal pores, twenty on each side, bordering posterior edge of a glandular swelling on undersurface of thighs. Hemipenial swellings covered with somewhat enlarged scales; a series of about 104 widened subcaudal scales; occasional ones divided. Tail segmented, segments marked by transverse series of six enlarged tubercles, with a secondary transverse row also indicated on basal segments; digits moderately widened with a narrow web remnant on hand and foot; terminal phalanges of four outer digits somewhat compressed, bearing claws; inner digit lacking claw; about 20 lamellae under longest toe, basal ones segmented into three or four parts; postanal sacs present, openings evident behind vent.

Color in life: Above cream, with a brownish wash, becoming darker in preservative; cream to yellowish below; top of head with

two diagonal elongate spots bordering occiput, widened mesially; other indistinct spots or flecks of black on occipital and interorbital regions; back with nine or ten small irregular paired spots; some spots on base of tail, the distal portion banded in black and cream; many dorsal tubercles are cream. Lower surfaces whitish or cream-white.

Measurements in mm.: Snout to vent, 80; tail, 104; width of head, 17.2; length of head, 22; snout to arm, 28; axilla to groin, 37; arm, 23.5; leg, 35.

Variation: The number of supralabials and infralabials varies from 10 to 13; the number of femoral pores from 16 to 20 on each side. The apparent amount of pigment in the scale changes, individuals taken at night being lighter in color.

Distribution: The species enters Thailand in the extreme south. A specimen is known from Narathiwat,* Narathiwat. Elsewhere it is known in Malaya and the Indo-Australian Archipelago to the Philippines.

Remarks: The species is nocturnal and its call is heard most frequently at twilight. It is occasionally seen in human habitations that are close to forest. It is not a typically domestic form such as *Gekko gecko,* however, Boulenger (1912) states "Very common in houses in Singapore." I obtained many from a house on Maxwell's Hill in Perak, but none elsewhere in houses.

Gekko gecko (Linnaeus)

Lacerta gecko Linnaeus, Systema naturae, Ed. 10, 1758, p. 205 (Certain subspecies are recognized one of which occurs widely in Thailand).

Gekko gecko gecko (Linnaeus)

Fig. 28

Lacerta gecko: Linnaeus, Amoen. Akad., Tom. 1, no. 5, p. 133; Linnaeus, Systema naturae, Ed. 10, 1758, p. 205 (type-locality "habitat in Indiis"); Anderson, Bihang Sven. Vet-Akad., Band 26, Afd. 4, no. 1, 1900, pp. 13-14.

Gekko verticellatus Laurenti, Specimen medicum, exhibens synopsin reptilium emendatum . . ., 1768, p. 44 (Based on Seba, Thesaurus, vol. 1, pl. 108, figs. 2, 6 (type-locality, India); Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 183; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 102; Flower, Proc. Zool. Soc. London, 1899, p. 631; de Rooii, The reptiles of the Indo-Australian Archipelago, vol. 1, 1915, pp. 56-57, figs. 33a, 34, 35; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, pp. 52, 152 (Klong Wang Hip, Nakhon Si Thammarat).

Gekko gecko: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 111-112, fig. 32.

* The specimen was collected at "Bangnara, Patani" (now in the province of Narathiwat) by Mr. C. J. Aagaard.

FIG. 28.—*Gekko gecko gecko* Linnaeus. No. 4028 Chiang Mai city. Total length, 292 mm. Tail partially regenerated.

Platydactylus guttatus Duméril and Bibron, Erpétologie générale . . ., vol. 3, 1836, pp. 328-331; Daudin, Histoire naturelle des reptiles, vol. 4, 1802, p. 122, pl. 49 (type-locality unknown).

Gekko indicus Girard, U. S. Exploring Expedition, herpetology, 1858, p. 290, pl. 16, figs. 9-16 (type-locality, Island, in Balabao Strait, China Sea).

Diagnosis: A large domestic and forest species reaching a length of about 350 mm. Head large covered with small polygonal scales; male with five to twelve preanal pores on each side forming a median wide angle; small scales above intermixed with series of larger tubercles. Gray to ultramarine above, with brick- or orange-red spots and numerous gray-white spots; digits entirely free with numerous undivided lamellae on undersurface.

Description of species (from No. 440, Khao Chong Forest Experiment Station, Trang): Large-headed species; rostral nearly twice as wide as high, subrectangular, notched above mesially and with a small entrant suture, bordered laterally by a supralabial and behind by two prenasals and a single internasal; nostril separated from rostral, surrounded by the prenasal, two supranasals, two postnasals and first labial; eighteen granular scales across snout between third supralabials; supralabials 13-14, followed to mouth-angles by undifferentiated scales; infralabials eleven; mental small, with a labial border much smaller than that of rostral; median pair of chinshields in contact throughout most of their length; on each side of these, three scales touching infralabials; scales in occiput and interorbital regions small, subequal, about 21 between median supraciliary edges; auricular opening vertically placed, tympanum deeply sunk; scales on swollen portion of lower jaws larger than those on median parts of chin and throat.

Dorsal scales on body, tail, and above limbs, small intermixed with conical tubercles forming 12-14 indefinite rows; on tail they are arranged in transverse whorls, one to each tail segment together with six to eight rows of smaller scales. A pair of ventrolateral folds separated by 24 rows of scales not or scarcely imbricate. Median subcaudal scales somewhat enlarged, paired; a somewhat angular series of ten imperforate preanal scales (represented by pores in males).

Digits with a slight basal web, each covered below with widened undivided lamellae, 20 under longest finger, and 22 under longest toe followed by three or four flat scales; distal phalanx and claw arising from widened terminal portion; inner finger and toe lacking claws and distal joint.

Color in life: Above ultramarine, head with numerous rusty-red

spots; back and sides with scattered rusty-orange spots, and an indefinite series of gray or very light ultramarine spots forming five or six transverse bands across back, the spots often confluent; tail dimly banded in dark and light ultramarine. Chin and venter with some indefinite orange flecks on a gray-white background; lamellae under digits blackish.

Measurements in mm.: Snout to vent, 134; tail (tip regenerated), 114; snout to arm, 47; axilla to groin, 69; head width, 30; head length, 41; arm, 43; leg, 52.

Variation: The variation in this species is not great, except that the number of preanal pores varies between 10 and 24. The color may be gray, or violet-gray. The markings in the young specimens are more distinct, the tail being banded with blue and white. The ventral spotting may be pinkish or rusty-red as well as orange.

The largest specimen I have seen measures 185 mm. snout to vent, the tail 179, totalling 364 mm.

Distribution: With the possible exception of high mountains the species is ubiquitous within Thailand. Outside the country the species is widespread from northeastern India, through southern China, Thailand, Indo-China, Malaya, and the Malayan Archipelago to the Philippines.

Remarks: The presence of this species is often made known by a series of loud sounds, variously interpreted as Tuk-ko—Tuk-ko, repeated several times, and usually preceded by a "cackle" and often terminating in a low gurgle sometimes sounding like a laugh. While the call is usually given at night or in the evening, it occasionally can be heard during daytime.

Many legends have grown up about this striking domestic species. The one that is repeated most frequently relates that the lizard holds his mouth open (a characteristic defense attitude) so that a snake (a friend) may eat of its liver which has grown so large that it pains the animal. The particular kind of snake involved varies from place to place. One should of course realize that such folklore is fiction and not scientific fact.

The biscuit-shaped eggs are plastered together and against a surface, usually in some dark place, and left to hatch. Each female lays only two hard-shelled eggs at a single laying. Frequently several females will deposit their eggs together in the same place.*

* In an ancient burial cave on Tablas Island, in the Philippines, whose "top" had very recent slipped off into the sea, I found that all the skulls in the exposed burial jars were filled with the egg-shells of this species. Many eggs were plastered on the shells of eggs already hatched.

Gekko smithi Gray

Fig. 29

Gecko smithi Gray, Zoological Miscellany, May, 1842, p. 57 (type-locality, "Prince of Wales Island" = Penang); Stoliczka, Journ. Asiat. Soc. Bengal, vol. 39, 1870, p. 161, and vol. 41, 1872, p. 92; Anderson, Proc. Zool. Soc. London, 1871, p. 159.

Platydactylus stentor Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 624 (type-locality, Penang Island); 1847, p. 18 (separate of the above).

Gecko stentor: Günther, Reptiles of British India, 1864, p. 102, pl. 11, fig. A; Boulenger,* Catalogue of the lizards in the British Museum, vol. 1, 1885, pp. 184-185 (Penang, Andaman Is. Borneo, Sumatra); Fauna of British India; Reptilia and Batrachia, 1890, p. 103, (Burma, Malay Peninsula, Java); Fasciculi Malayenses, Zool., vol. 1, 1903, p. 150; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 51; M. Smith, Bull. Raffles Mus., Singapore, no. 3, Apr. 1930, p. 18 ("Patani," Thailand).

Gecko verreauxi Tytler, Journ. Asiat. Soc. Bengal, vol. 33, 1865, p. 546 (type-locality, Andaman Is.).

Gecko albofasciatus Günther, Ann. Mag. Nat. Hist., ser. 3, vol. 20, 1867, p. 50 (type-locality unknown).

Gekko smithi: M. Smith, Fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 111-112.

Diagnosis: One of the largest geckoes, reaching a length of 340 millimeters. Throat with minute granules; preanal pores 11 to 16; each tail segment with 10-11 transverse rows of scales; usually two series of enlarged subcaudals. No reddish spots; rostral fails to border nostril.

Description of species (from EHT-HMS M. 225): Head large, snout length greater than distance between eye and ear-opening. Rostral low, nearly twice as wide as high with an upper entrant suture, bordered laterally by supralabials, posteriorly by a prenasal and a supranasal that lie largely in front of nostril separating rostral from the nostril border, and a small median internasal; nostril bordered by first supralabial, prenasal, supranasal, and three postnasals; nostril elongate, oval; supralabials, 14-16 last very small, followed on labial border by twelve or more small granules which are bordered above by four larger scales; infralabials, 11-11; mental with a smaller labial border than rostral; pair of moderately elongated median chinshields, each followed by a series of five or six chinshields or sublabials in contact with infralabials; auricular opening moderate (diameter, 4 mm.) separated from eye by a distance more than three times its diameter.

Scales on sides and front of snout rounded, juxtaposed, many with a tiny median elevation; smallest in the shallowly concave frontal

* Günther and Boulenger (1885) did not accept Gray's name, the latter stating that it was inadequately described—"no proper description." However by present definition of "proper description" this name must be used. Malcolm Smith reinstated the name in 1935 (*loc. cit.*). I follow him in this usage.

FIG. 29.—*Gekko smithi* Gray. EHT-HMS No. M.16 (2160) Kepong Forest Reserve, Selangor, Malaya. Actual snout-vent length, 161 mm.; total length, 309 mm.

and occipital areas; scales above eyelids nearly as large as those on snout; scales on dorsum small, juxtaposed, with 12 rows of large flat rounded tubercles (rarely conical), the rows somewhat irregular, growing gradually smaller as they approach the occipital concavity.

Scales on chin very small, juxtaposed, those on venter larger, cycloid, imbricating; a pair of ventrolateral skinfolds; scalerows between folds on venter about 24; near middle of venter two rows are fused to produce a row of widened scales that continues for a short distance. A transverse series of seven preanal pores, the scales not enlarged more than adjoining rows.

Tail segments strongly marked by transverse series of tubercles, eight on basal segments six on intermediate segments and four more distally, each segment also has about eight or nine rows of small scales; subcaudal scales paired, transversely widened (occasionally single scales). Total subcaudal pairs approximately 103. Tubercles present on forearm but more on upper arm; present also on dorsal part of thigh and tibia; fingers and toes with widened lamellae under proximal parts; near middle of widened portion of digit, distal phalanges arise at an angle and extend forward but attached to the widened part by a web as far as its anterior edge.

The terminal joint and claw absent on inner finger and toe; a small basal web or web remnant between middle digits. Twenty lamellae under longest digits of hand and foot; 15 to 17 under inner digits. Adpressed legs reach elbow; two large tubercles on sides of tail-base (male).

Color: Above gray with eight transverse rows of white tubercles on body, first two tending to form curved series on back of occiput. Venter gray-white the tail gray below; above banded with light gray and dark gray.

Measurements in mm. (Nos. EHT-HMS M. 16 and M. 225, respectively): Snout to vent, 161, 172; tail, 148, 155; * snout to arm-insertion, 57, 62; axilla to groin, 76, 85; width of head, 31.5, 35.8; length of head, 40, 47; arm, 47, 54; leg, 68, 73.

Variation: The number of supralabials varies from 12 to 16, the infralabials from 10 to 12, the variation being chiefly in the small posterior scales of the series. In the younger specimens the dorsal tubercles appear somewhat conical. Preanal pores vary from 7 to 16; this may be, in part, geographical variation, however, in two specimens from Selangor, one has 7, the other 12 pores. There are

* Terminal 80 mm. reproduced. Both specimens from Selangor.

three prominent moundlike tubercles on each side of the base of the tail.

In No. M 16 the supranasal on each side is divided and a separate prenasal stands between the rostral and the nostril.

Distribution: In Thailand the species has been taken only in "Patani" = Narathiwat.

It is known also in Malaya, Burma, Sumatra, Borneo, and Java. The type-locality is Penang.

Remarks: The species is arboreal usually keeping to tall forest trees. I have seen individuals of the species on two occasions in Johore, Malaya and once in a tree near Bhetong, Yala Province, Thailand. All were at considerable elevation and all escaped.

Genus PTYCHOZOON Fitzinger *

Ptychozoon Kuhl, Isis, 1822, p. 475 *(nomen nudum)*; Fitzinger, Neue Klassification der Reptilien nach ihren natürlichen Verwandtschaften; Wien, 1826, p. 13 (type of the genus *Lacerta homalocephala* [= *P. kuhli* Stejneger]).

Diagnosis: Digits strongly webbed, dilated, the lamellae below transversely widened and not divided; terminal phalanges of outer four digits on hand and foot bearing claws but more or less attached to the widened part; terminal phalanges and claw absent from inner finger and toe; dorsal squamation consists of small scales or with small scales and enlarged tubercles; a skin-flap on sides of head, one on sides of body, while the skin expansion on tail is divided into numerous separate scallops, the terminal portion of which may be widened into a single enlarged flap. Pupil vertical; male with preanal and/or femoral pores.

Two species have been found in Thailand, a third occurs in Malaya at approximately the same latitude as the southern border of Thailand and it most probably occurs also in that country. The species may be differentiated by the following key:

KEY TO SPECIES OF PTYCHOZOON

1. Male with preanal and femoral pores separated; no enlarged dorsal tubercles; tail tapering gradually to tip, scallops on tail smaller and directed somewhat backwards; no enlarged tubercles (not known in Thailand) ..... *horsfieldi*
2. Dorsal body scales intermixed with larger tubercles; preanal pores, 20-25; tail widened at tip into a flap, the scallops wider than in *horsfieldi* and placed at right angles to axis of tail ..... *kuhli*

   Males with from 16-25 preanal pores; no enlarged tubercles intermixed with dorsal body scales; scallops narrow directed somewhat backwards; tail not forming a widened flap at tip ..... *lionatum*

* Kuhl's use of this name seems to be *nomen nudum*. Fitzinger places *P. homalocephalum* as the single species in the genus hence it becomes the type of the genus by monotypy.

These species are nocturnal, hiding by day in dark crevices or inside the trunks of hollow trees, occasionally entering buildings constructed in forested areas.

One might suspect that *lionatum* and *kuhli* were geographical forms of the same species since the former occurs in northwestern Thailand where the latter is unknown. However, both species occur in the mountains only a few miles apart and at about 300 meters elevation in the southern part of the province of Nakhon Si Thammarat.

I have observed an individual *P. intermedium* jump from a point on a tree at an elevation of eight feet, land on the ground some ten feet from the tree, remain motionless, quickly becoming much darker in color and nearly invisible in dark surroundings. The lateral flaps on the body were expanded in flight.

Two eggs are placed under bark or on the boles of trees where the sun seemingly cannot reach them. The eggs are biscuit-shaped, usually plastered to the surface of smooth-barked trees and to each other. I obtained a double-headed embryo of *P. intermedium* on a tiny islet in the Sulu Archipelago from one of two such eggs found under dead bark.

Ptychozoon lionatum Annandale

Fig. 30

Ptychozoon homalocephalum Cantor (*part.*) Journ, Asiat. Soc. Bengal, vol. 16, 1847, p. 626; Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 316 (*part.*).

Ptychozoon homalocephalum var. *lionatum* Annandale, Ann. Mag. Nat. Hist., ser. 7, vol. 15, 1905, p. 30 (type-locality, Pegu, Burma).

Ptychozoon lionatum: M. Smith, The fauna of British India, . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 118-120.

Diagnosis: Head and body flattened, with a skin-flap on side of head below ear; a lateral skin-flap extending on side from axilla to groin; other skin-flaps on front of arm, upper anterior part of tibia, posterior part of thigh and posterior edge of tibia; digits strongly webbed; lamellae under distal part of digits transversely widened and undivided; inner digits lacking distal phalanges and claw; preanofemoral pores, 15-16, present in males; tail tapering to tip, the lateral dermal flap scalloped; no enlarged dorsal tubercles intermixed with body scales; small scales present on underside of lateral skin-flap.

Description of species (from No. 35538, Khao Chong Forest Station, Trang, May 22, 1958; taken at night on a pavilion near waterfall): Rostral 4.2 x 2.1 mm., subrectangular, bordering nostril, first supralabials, two supranasals, and an internasal nearly as large as

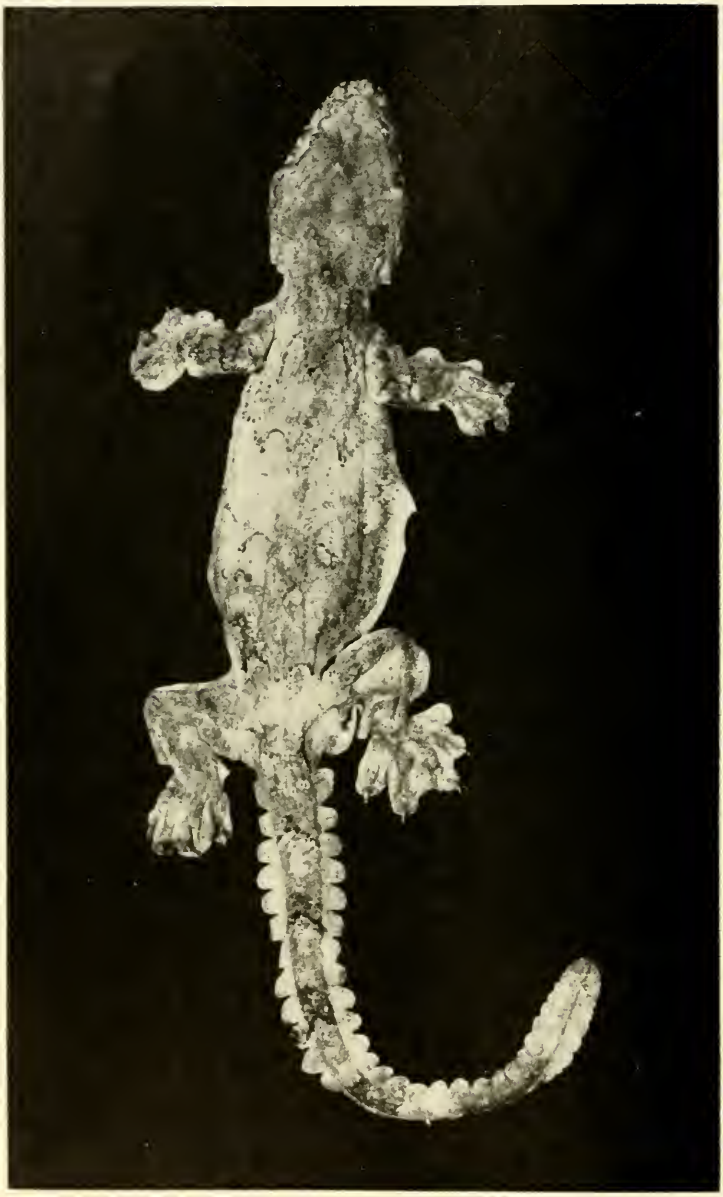


FIG. 30.—*Ptychozoon lionatum* Annandale. Khao Chong Forest Experimental Station. Trang province, Thailand. Actual total length, 161.5 mm.

anterior supranasal; a straight vertical median suture in upper part of rostral; rostral borders nostril above and in contact with two scales the upper one of which also borders nostril; a single large postnasal and first supralabial complete nostril border; about 32 scales across snout between sixth supralabials; supralabials, 13-14, posterior ones much reduced in size, and series followed by smaller scales to mouth-angle; infralabials, 11-11, followed by several small scales to mouth-angle; mental small, its labial border scarcely half that formed by rostral; a pair of median chinshields less than twice as long as wide, in contact for five sixths of their length; second pair of chinshields about half size of first pair, separated by first pair; three succeeding pairs separated by preceding chinshields becoming gradually smaller, fourth pair separated from each other also by about 17 granules; sublabial scales following somewhat enlarged; a patch of enlarged scales on lateral skin-flap below ear-opening; greatest width of flap 4.15 mm.; a slight depression behind nostril; a slight interorbital depression extended somewhat on frontal region; scales on snout larger than those in interocular, and occipital regions; scales on dorsum small, nearly uniform, somewhat rounded, pavementlike; no enlarged tubercles intermixed either on body, head, or limbs; lateral skin-flap with transverse series of five to eight enlarged scales and two to four smaller distal rows; underside of flap with small granules; other skin-flaps on limbs with patches of enlarged scales; venter with about 68 rows of cycloid, imbricated scales; seven or eight preanal rows of scales following a slightly angular row of twenty pore-scales, some with depressions (female); (male with as many pores); tail segmented, each segment bearing a free flap or united at base with succeeding flaps; distally flaps are united for most of their length; terminal ones being scarcely indented on their edges; scales above each segment forming seven to ten transverse rows; subcaudal scales enlarged, median pairs largest, usually four rows to a segment; approximately 28 segments, terminal ones of last four millimeters of length not clearly differentiated; digits with transverse lamellae, 17 or 18 under fourth finger and toe, distal ones widest and slightly angulate; webbing extends to widest point on distal part of digits; two distal joints of digit tend to form an angle with remainder of digit and fused with widened part below it; two last joints with claw, absent from inner digits; about 94 granules from chinshields to a line drawn between shoulders; approximately 94 scales from breast to vent; postanal slits present; upper and lower borders of vent, smooth, liplike.

Color and markings: Dull gray-lavender with four narrow transverse brown marks, which are sinuous or lobulated; head nearly uniform gray-lavender; supra- and infralabials nearly white with some sutures between scales edged with black; tail with several spots or bands, their posterior edges angulate, becoming elongated distally; chin, throat, and breast whitish, with very little scattered pigment; venter with denser pigmentation; subcaudal region with dark bands, posteriormost longest; distal part of body-flaps lighter in color than proximal parts.

Measurements in mm.: Total length, 161.5; snout to vent, 80.5; tail, 81; length to arm-insertion, 29; axilla to groin, 39; length of head, 24.6; width of head, 16.3; greatest width of body-flap, 7.1; arm, 24; leg, 32.

Remarks: This specimen was found about 1 o'clock at night on a small pavilion built near a waterfall at Khao Chong Forest Station. It was the only specimen taken. Another *Ptychozoon* presumably of this species was discovered near the summit of a small dead tree whose top was broken. The specimen after considerable disturbance from a long bamboo pole took "flight" jumping the gap of approximately 2.5 meters between this and another living tree partly covered with vines and aerial plants. It landed on the trunk at an elevation of perhaps 15 feet lower than the point of departure. The specimen found a hiding place from which I was unable to dislodge it.

The "flight" was unexpected and so sudden that I cannot vouch for the condition of the lateral flaps. It is, however, my impression that they expanded in flight. This species lays two eggs which are at least occasionally plastered on the outerside of smooth bark of living trees.

Ptychozoon kuhli Stejneger

FIGS. 31, 32, 33

Lacerta homalocephala (not of Suchow 1798) Creveldt, Mag. Ges. Naturf. Berlin, vol. 3, 1809, p. 267, pl. 8. (Type-locality ?)

Gecko homalocephalus: Tilesius, Mem. Acad. St. Petersburg, vol. 7, 1820, pl. 10.

Ptychozoon homalocephalum: Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 626 (*part.*); Günther, Reptiles of British India, 1864, p. 105; Stoliczka, Journ. Asiat. Soc. Bengal, 39, 1870, p. 159; Baur, Proc. Zool. Soc. London, 1885, p. 718; Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, pp. 190-191 (*part.*); The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, pp. 104-105, fig. 31 (*part.*); Fasciculi Malayenses, Zool. 1, 1903, p. 150; Journ. Federated Malay States Mus., vol. 3, 1908, p. 64; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 52-53; De Rooij, Reptiles of the Indo-Australian Archipelago, Leiden, vol. 1, 1917, p. 58.

Ptychozoon kuhli Stejneger, Proc. Biol. Soc. Washington, vol. 15, 1902, p. 37 (new name); Mertens and Senfft, Nat. und Mus., Frankfurt am Main, vol. 59, 1929, pp. 218-224, figs. 1-4; Mertens, Blatt. Aquar. Terrar.-k, Jhr. 40, 1929, Heft. no. 6, p. 104; M. Smith, Bull. Raffles Mus., no. 3, Apr. 1930, p. 19; The Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 117-118, fig. 34; Tweedie, Proc. Zool. Soc. London, 1950, vol. 120, p. 13 (Pl. 1, photo); Bull. Raffles Mus., no. 25, 1954, p. 107-109, pl. 1, text fig. 1.

Diagnosis: Body flattened; skin-flaps present on side of head, front and posterior part of arms, front and posterior part of legs, on side from axilla to groin, on sides of tail; toes webbed, widened lamellae under digits undivided; terminal joints and claw absent from inner digits; preanofemoral pores, 21-26. Dorsal tubercles with several irregular rows of large flat rounded, or somewhat conical tubercles intermixed; tail segments with a transverse series of six (basally), four or two enlarged conical or trihedral tubercles intermixed with smaller scales of tail segments. Lateral body flap with separated lines of scales on its underside; a very short indistinct suture enters upper edge of rostral.

Description of species (from 35537, collected approximately 10 km. west of Nakhon Si Thammarat, May 3, 1958): Rostral nearly quadrangular (5 mm. x 2.2 mm.), with a short groove or suture entering from above, scarcely more than .3 mm. in length; rostral borders first supralabials and a pair of widened supranasals; nostril surrounded by rostral, anterior supranasal, a posterior supranasal, first labial, and a postnasal; anterior internasals form median suture, each bordered posteriorly by three scales, median pair largest; about 30 scales in a row across snout between third labials; approximately 64 scales between seventh supralabials across snout; supralabials, 13, posterior ones very small, and followed by a row of eleven or twelve small scales to angle of mouth; infralabials thirteen, anterior ones much larger than supralabials, reducing in size posteriorly and followed to mouth-angle by six or seven small scales; first pair of chinshields about twice as long as wide, in contact for over four fifths of their length; second chinshields about half size of first; these followed by three others of about same size; granules on chin and throat, from chinshields to a line in front of shoulders, about 100; from this point to vent about 105 scales on median line.

Scales on head variable in size, largest on frontal region and in front of orbit; smallest scales in occiput, without enlarged intermixed scales; dorsal scales small, subequal on sides, median rows a little the larger, with several rows of enlarged, rounded, sometimes subconical tubercles intermixed, chiefly in posterior part of body; scales on side below skin-flap granular for about 39 rows, while

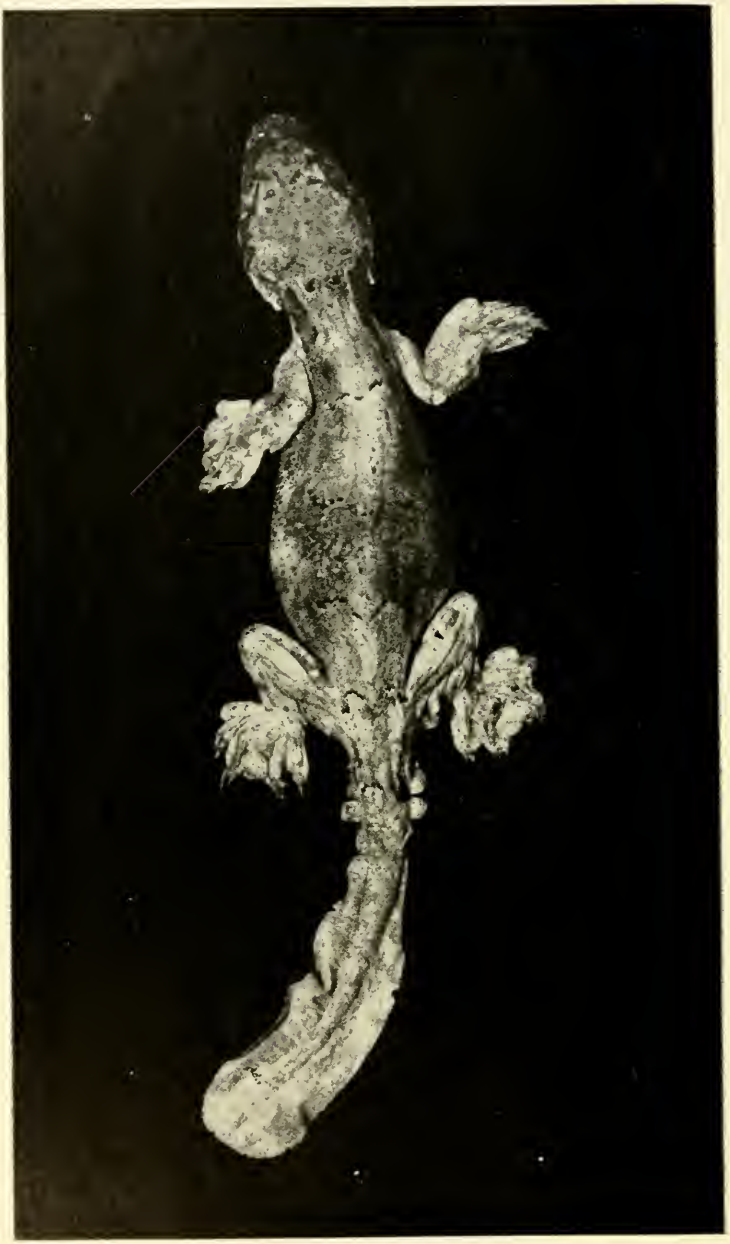


FIG. 31.—*Ptychozoon kuhli* Stejneger. No. 35537, 10 km. west, Nakhon Si Thammarat, city. Actual length, 157 mm.

median ventral 26 to 28 rows of scales, enlarged, flat, cycloid, imbricating; a transverse, slightly angular row of 26 preanofemoral pore-scales, followed by five or six rows of somewhat enlarged preanal scales; tail segmented at base (greater part of tail regenerated and unsegmented) (normally segmented throughout); upper part of tail segments normally with 12-13 irregular rows of small scales, intermixed with six (four, or two on distal parts) enlarged trihedral or conical tubercles in a transverse row; subcaudal scales enlarged, about five rows to each segment subcaudally, median series partly paired or partly irregular.

Scales above ear-flaps about size of, or a little larger than, ventral scales, with smaller scales on under surface of flap; lateral body flap, 15 mm. wide; above, scales arranged in transverse series, the undersurface largely without any scales; basal part of tail with each segment bearing a small separate flap standing at right angles to axil of tail. (Normally at least 17 segments show scallops) but the terminal part of the tail (latter third or fourth) forming a widened flap.

The regenerated tail has a continuous flap, narrow proximally (9.5 mm.) but growing wider distally on last 30 or 40 mm. of length.

Ear-opening moderately large, its diameter 2.7 mm.; ear to eye, 8 mm.; length of snout, 10 mm.; diameter or orbit, 7.5 mm.; lamellae under digits widened distally, undivided, basal part with eight or ten scales; total scales and lamellae, 25 under fourth finger, 31 under fourth toe.

Color in life: Above brownish to gray-lavender with a series of blackish spots across nape of neck, and with a longitudinal series of dark flecks back to above arm-insertion; four narrow sinuous marks across back usually bordered by black on anterior edge; chin, throat, and venter dirty white somewhat darker under thighs and subcaudal region; head nearly uniform gray-brown above; lateral flaps with indefinite blackish color proximally; ear-flaps much lighter than other skin appendages.

Measurements in mm. (of Nos. 35537 and 35631*: Snout to vent, 94, 32; tail, 63 (regenerated), 27.4; total length, 157, 59.4; snout to arm-insertion, 34.6, 16; axilla to groin, 42, 14; head width, 19.6; 8.7; head length, 28, 12; arm, 37.5, 11; leg, 41, 15; width of body-flap, 17.2, 4.5.

* Two biscuit-shaped eggs of this species were discovered plastered behind a small board, nailed on a tree. The eggs measured approximately 16 x 16 x 6.8 mm.; both were broken when they were being removed. An embryo measuring about 59.4 mm. was removed from one of the eggs, a mass of yolk remained. The animal had the characteristic gray and black markings of the adult. They would appear to be larger on hatching than the young of *lionatum*.

Variation: The supralabials vary between 11 and 15, the infralabials between 10 and 13. The enlarged tubercular scales may extend as far forward as the occiput. The preanal pores vary between 20 and 26.

Distribution: *Ptychozoon kuhli* has been taken at Bukit Besar (near Na Pradoo), Pattani; and 10 km. E of Nakhon Si Thammarat. The species is known in Malaya, in Sumatra, Borneo, Java, and the Nicobar Islands. *Ptychozoon horsfeldi* has been taken at Penang, Malaya, and probably may occur in southern Thailand.

FIG. 32.—*Ptychozoon kuhli* Stejneger. Khao Chong Forest Experiment Station, Trang province, Thailand. Embryonic specimen taken from egg. Actual total length, 59.4 mm.

Remarks: The female specimen described was found in a dark narrow crevice between two close-growing branches. It was routed from this place by aimless probing into the crevice with a small strip of bamboo. There are two large eggs in the body presumably nearly ready for deposition.

Malcolm Smith has commented that *lionatum* is very closely allied to *P. kuhli.* "I have examined seven specimens including the types. The preanal pores vary from 16 to 25 in number. The coloration is variable and much as in *P. kuhli.*"

The specimen which I have described as *lionatum* occurs in the same area as *P. kuhli* and they very probably will be found to occur together.

There are several characters in which *P. kuhli* differs from *lionatum.*

1. Presence of enlarged dorsal tubercles (none in *lionatum*).
2. Widening of the terminal tail flap (narrowed in *lionatum*).
3. Slightly different slant of the caudal scallops.
4. The lateral flap considerably wider, sometimes twice as wide.
5. Tail with six (basal segments), four or two large trihedral tubercles on tail segments (none in *lionatum*).
6. The rows of ventral granular and cycloid scalerows number about 106 (about 68 in *lionatum*).
7. The supranasals are in contact (separated in *lionatum*).
8. Conical tubercles in transverse rows on each tail segment; (no conical scales in *lionatum*).

There are many other less obvious differences. Thus it seems certain that these forms merit specific distinction.

The tail of No. 35537 has been regenerated for more than half its length without evidence of segmentation.

Addenda: A specimen of *Ptychozoon* from the high mountains of Chiang Mai, cannot be properly allocated since it lacks a tail; as no Thai specimens are known in that region it may represent an undescribed race or species (figured).

FAMILY AGAMIDAE

The populous family of the Agamidae has its counterpart in the family Iguanidae. Often a genus of one of the families appears to take on the characteristics of a genus of the other so that superficially it may be difficult to determine its true relationship. Many authors have commented on this.

Opinion seems to be divided as to whether these resemblances

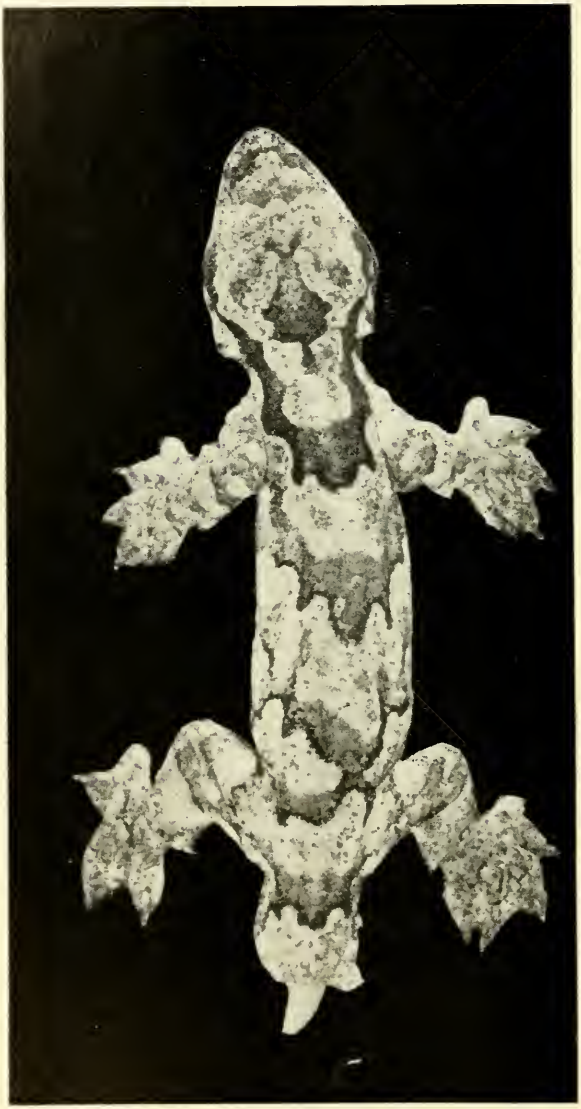


FIG. 33.—*Ptychozoon* sp.? EHT-HMS, No. 265. Photo of a specimen lacking tail, from the high mountains of northern Chiang Mai. Without the tail its identity cannot be satisfactorily established. Collected by Oliver Gordon Young, 1961.

are because of a close relationship of the families or because of some inherent pattern in heredity or adaptation. The Agamids are largely confined to Asia, Australia, and Africa; the Iguanidae to the Western Hemisphere. However, there are some anomalous facts. The Agamids, while present in Africa, are absent in Madagascar and New Zealand, which represent breaks in the continuity of their distribution. The Iguanids have a continuous distribution in the Western Hemisphere but they also appear in Madagascar and certain islands in the Pacific.

The dentition of the two families differs and is perhaps the major character for warranting familial differentiation between the two groups.

Only a few genera (*Physignathus*, *Uromystax*, and *Leiolepis*) have the typical femoral pores of lizards. While of different origin and structure, species of certain genera have in the preanal region or on the posterior part of venter, callose scales with epithelial tissue that accumulates and which can be removed from the scale, leaving a pit.

Adaptations to habitats are marked. Slow-moving terrestrial forms usually display short legs and a flattened body; arboreal forms have the bodies compressed with a tail often three to four times greater than the length of the head and body. Certain fast moving terrestrial forms have the legs greatly enlarged and bipedal movement is often assumed. An elongate tail is present, and curled up high appears to serve as a balancing organ when the animal is running in a bipedal manner.

One curious habit of a number of species of agamids is that after a hole is dug for deposition of eggs, the earth used to cover the eggs is pounded using the head as a pile-driver.

While most forms lay leathery eggs that have the oval shape of most reptilian eggs, some species of certain genera (*Calotes*) may lay spindle-shaped eggs. The eggs of certain species of *Draco* have a tiny terminal shelf at one end.

Unlike in many genera of the Scincidae and Teiidae there is little tendency for the competition for food between two species, to drive the weaker competitor underground, with the consequent loss of digits and limbs. In this family practically all forms are typically pentadactyl. An exception however, is a Ceylonese and Indian genus *Sitana* comprising a single species, which has lost the fifth toe. There are no snake- or wormlike forms.

The food, at least in the smaller forms, is chiefly insectivorous. In a few larger species of the family, *i. e., Lophura* and *Leiolepis*, the animals are at least primarily herbivorous. *Lophura*, which feeds chiefly in trees near streams or bodies of water, has become at least semiaquatic; and often when disturbed takes refuge by diving into water from the trees where they are feeding. They usually swim under water.

In Thailand, *Leiolepis* is often offered in the food markets for human consumption.

The skulls of the Agamidae are well ossified, and the dentition is confined to the jaws, none of them having palatal teeth. The character of the teeth in many but not all species varies somewhat in the manner of Mammalian teeth, and we may liken them to incisors, canines, and molars. The molar series is ankylosed to the bone of the jaw and the teeth themselves may be joined together solidly at their bases forming an uninterrupted row. The canines are distinct and the incisors are more or less fused. The teeth for the most part are not replaced.

There are no enlarged symmetrical head-scales such as occurs in several families of lizards. Nor are there osteoderms as is common in certain families (Scincidae). The head is covered with very numerous scales, the general pattern of their distribution being symmetrical on the two sides. The shape and character of the individual scales vary remarkably. Many forms have small glands in the scales, especially those of the head, and many forms have a fine hairlike process extending back from the posterior part of the scale. In many species the scales are keeled and may bear mucrones.

Seven genera of the family Agamidae are represented in Thailand. Some species at least, have a fairly wide distribution in the country. The exceptions are largely in the genera *Draco*, *Goniocephalus* and *Aphaniotus*. The last two genera are presumably confined to the southern part of peninsular Thailand, and several of the species of *Draco* are likewise confined to the same area.

KEY TO THE THAI GENERA OF AGAMIDAE

1. Five or six elongated ribs supporting lateral dermal expansions serving as wings for gliding flight; a longer or shorter gular projection (dewlap) at least in males; arboreal . . . . . *Draco*
   Ribs not supporting a dermal expansion for gliding flight; sometimes a small gular pouch but no typical dewlap 2
2. Femoral pores present in males 3
   Femoral pores not present 4

3. Femoral pores (at least in males) four to eight on each side; tail strongly compressed, covered with small keeled scales above, and much larger, more strongly keeled ones below; leg reaches to eye or tip of snout; large ..... *Physignathus*
   Femoral pores (at least in males) 13-21 on each side; tail thick at base somewhat flattened, covered with small equal keeled scales the largest ones in subcaudal region ..... *Leiolepis*
4. Tympanum hidden; no gular fold or pouch; inside of mouth blue, *Aphaniotus*
   Tympanum exposed; mouth lining not blue; small gular-fold sometimes present 5
5. A strong spine arising behind orbit and one on side of neck, *Acanthosaurus*
   No strong spine arising behind orbit, or on side of neck 6
6. Dorsal scales unequal, intermixed with few or many larger irregular scales; a high dorsal crest in males, the crest somewhat lower in females ..... *Goniocephalus*
   Dorsal scales (in Thai forms) nearly uniform, not intermixed with larger scales; body scales regularly arranged ..... *Calotes*

Genus DRACO Linnaeus

Draco Linnaeus, Systema Naturae, 1766, vol. 1, p. 358 (type species, *Draco volans* Linnaeus).

Diagnosis: Five or six elongate ribs passing through body wall, supporting a wide membrane continuous with body skin, that may be folded parallel to body or expanded like a fan by rib movements; body somewhat depressed with an elongate tail depressed at base, but usually more or less compressed elsewhere; a gular appendage (dewlap), large in males, small or nearly absent in females; a small winglike membrane bordering side of head and neck (wattles); tympanum scaled or naked; a pair of caninelike teeth in both upper and lower jaws; legs short; no femoral pores.

The genus *Draco*, confined to India, Southeastern Asia and most of the Indo-Australian Archipelago, has no less than thirteen forms in Thailand, where the species have the generic native name of *ginka bia*, this name being applied to all of the various forms.

The habits of the various dracoes do not seem to differ greatly. They usually are seen on tree trunks, the head pointed upwards, the body usually vertical, if at rest. The wings are usually folded except when in the air, although, the wing may be expanded during courtship, or during the process of shedding. Thus a specimen was seen after a shower expanding the wings to extreme capacity and holding them so for several seconds, then folding them. This was done a number of times. When the specimen was later captured, it was seen that the epidermis was broken in literally hundreds of

places the tiny patches producing the effect of whitish spots over the surfaces of wings and body. When dry the epidermal fragments were loose enough to be removed by the wind.

Some of the general structural characteristics are: enlarged scales above the nuchal wings (lappets or wattles); larger keeled scales on the front surface of the shoulders; frequently, but not invariably, a row of enlarged keeled separated tubercles, single or in small groups on the dorsum along the base of the wing-membranes; on the back edge of the thighs there is a series of enlarged, compressed overlapping scales which extends onto the adjoining edge of the tibia.

In the males of several species there is a longitudinal nuchal fold extending posteriorly from the back of the occiput for a variable distance on the neck. Sometimes some or all of the scales on the upperpart of the fold are serrate, sometimes not. The caudal crest, present in males of certain species, begins just behind the level of the vent, and continues along the median line of the dorsal surface of the tail, the scales forming distinct serrations. The nuchal and caudal crests attain maximum size in *Draco punctatus.*

When a median caudal crest is absent in a male there are usually two rows of slightly serrate scales on the dorsal surface of the compressed part of the tail. In species with caudal crests the females usually have three equal rows on the dorsal surface.

The insect food of the various species is seemingly extensively varied. However, certain forms in the Philippines would appear to feed almost exclusively on ants.

In many species four eggs are laid (*fimbriatus, taeniopterus, volans, formosus, maculatus,* etc.) but whether this is a fixed number for these and for certain other species, I do not know.

Draco melanopogon, on the other hand, presumably produces only two eggs. It is a smaller, slenderer species.

The wing may be described as being like a fan; the ribs penetrate the body wall remaining between two layers of skin which form the membranes of the wing. When the ribs are folded back, the wing is closed like a fan along the side of the body. The wings are used for gliding, the animal not being able to raise and lower the wing in the manner of a bird. The animal loosens its hold and starts to fall as the wings are opened. It may land at a lower point on the same tree trunk or on another tree, gliding a considerable distance if its goal is at a distance, changing direction when necessary to reach a particular tree.

The frequency with which a male and female are found together suggests that their mating may be a permanent one. Sometimes a male and female will leave a tree when disturbed and both alight close together on a tree twenty to fifty meters away. Occasionally when a female is near and the male is disturbed he will extend the dewlap and display its distinctive coloration several times. I have noted this particularly in a *Draco fimbriatus* although occasionally I have seen the same behavior in several other species.

The specimens in the forest are often difficult to see unless they happen to show a body profile at a proper angle against the light. Their coloring when wings are folded, blends with that of the tree so that in the forest light they cannot be discerned easily.

The appendage on the throat sometimes called a gular "pouch," is here called a dewlap, and the lateral nuchal wings are referred to as lappets or wattles for the sake of brevity.

The inverted Y-shaped series of scales on the snout may not be discernible in certain individuals of a species where it normally occurs. Other species where it does not normally occur may have a longitudinal series of two or three keeled scales on the median line of the snout.

The species when taken alive are very prone to bite, the sharp caninelike teeth usually penetrating the skin and in the case of the larger species, the bite can be painful. Contrary to certain beliefs, none of the species has a voice, and they make no calls of any kind.

The distribution of *Draco* in Malaya, Borneo and Sumatra shows that of the Bornean fauna of some 16 species, no less than eleven are common to the Malay Peninsula and seven also occur in Sumatra.

All species known in Malaya have been taken in Thailand except *Draco maximus* and this so far as I know occurs chiefly in the southern part of Malaya. It is known in Selangor and is relatively common in parts of Pahang. It should be looked for in Thailand.

KEY TO THAI SPECIES AND SUBSPECIES OF DRACO

1. Nostrils lateral, directed outwards 2
   Nostrils dorsal, directed upwards and often slightly backwards ... 6
2. Tympanum covered with larger or smaller scales 3
   Tympanum naked (*melanopogon* and *volans* occasionally have the tympanum at least partially covered with scales) 4
3. No blue spot * on each side of base of dewlap 3a

* The key given by Taylor and Elbel *loc. cit.* should read,
3. No blue spot on each side of base of gular appendage (dewlap) 4
   A blue spot on each side of base of dewlap 5

A blue spot on each side of base of dewlap 3b

3a. No spaced series of enlarged pyramidal or trihedral scales on side of neck continuous with spaced series at base of alar membranes; no caudal crest evident; a short nuchal crest, only the first three or four scales distinctly enlarged; underside of alar membranes yellowish with one or two black spots; to 87 mm. . . *maculatus maculatus*

A spaced row of enlarged trihedral scales on sides of neck continuous with spaced series at base of alar membranes; a small caudal crest evident; a nuchal crest involving 20-25 scales; underside of alar membranes yellow with numerous black spots; to 70 mm., *maculatus divergens*

3b. No series of pyramidal or trihedral scales along side of neck; alar membranes unicolor below lacking dark spots; base of dewlap deep orange; snout to vent 65 mm. ..... *maculatus haasei*

A series of pyramidal or trihedral scales on side of neck, curving above arm, continuous with the enlarged scales at base of alar membranes; nuchal crest barely indicated; dewlap blue at end, red behind its base; underside of alar membrane unspotted; to 86 mm., *maculatus whiteheadi*

4. Undersurface of wing bluish or ultramarine with rather ill-defined transverse series of irregular black spots; an inverted, Y-shaped series of enlarged keeled scales on front part of head; no caudal crest ..... *volans volans*

Undersurface of wing variable, but lacking transverse rows of black spots 5

5. Caudal crest present in males 6

Caudal crest absent in males 7

6. Dewlap of male saffron or orange, much longer than head; caudal crest present but not strongly defined ..... *fimbriatus fimbriatus*

Dewlap of male chrome-yellow, about same length as head; a very distinct nuchal crest; caudal crest with rather long vertically pointed scales ..... *punctatus*

7. Wing red, with five regular curved transverse dark bands each with a transverse row of small white dots, as wide as the intervening red spaces; a black band crosses underside of neck; narrow transverse blackish bands on undersurface of wing; body above dotted with blackish ..... *quinquefasciatus quinquefasciatus*

Body and wings not so colored 8

8. Dewlap deep black, longer than head; a light whitish or ultramarine posterior part; wings black dotted with numerous small yellow spots ..... *melanopogon*

Dewlap not black 9

9. Smaller species 75-85 mm. No caudal crest 10

Larger species 100-125 mm. A caudal crest 11

10. Scales on head very small, subequal on snout; dewlap about as long as head in males, covered with moderately enlarged scales; no maroon or magenta color on wing . . *haematopogon haematopogon*

Scales on head varied; an inverted Y-shaped series of enlarged keeled scales on front of head; a broad band of maroon or magenta on back part of wing; unspotted below; dewlap rounded, distally covered with large translucent scales . . *taeniopterus taeniopterus*

11. Distal two thirds of dewlap covered with large translucent scales; wings above olive or yellow-olive with fine lighter parallel longitudinal or slightly curving lines; orange to scarlet under wattles; immaculate yellowish under wing . . . . . *blanfordi*

Dewlap with large translucent scales. A caudal crest; wing membranes with irregular indefinite transverse dark curving bands; a broad band of maroon or magenta along back border, *formosus formosus*

Draco maculatus Gray

Four subspecies are recognized (see key).

Draco maculatus maculatus (Gray)

FIG. 34

Dracunculus maculatus Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 636 (type-locality, Penang Island, Malaya).

Draco maculatus: Günther, Proc. Zool. Soc. London, 1861, p. 187, The reptiles of British India, 1864, p. 125, pl. 13, fig. C (a Siamese specimen); Anderson, Anatomical and zoological researches . . . results of the two expeditions to western Yunnan in 1868, and 1875, London, 1879, p. 802; Blanford, Journ. Asiat. Soc. Bengal, 1878, p. 125; Boulenger, Catalogue of the lizards of the British Museum, vol. 1, 1885, pp. 262-263; *ibid.*, p. 492; A vertebrate fauna of the Malaya Peninsula . . . Reptilia and Batrachia, 1912, p. 58. M. Smith, Journ. Nat. Hist Soc. Siam, vol. 2, Dec. 1916, p. 152 (Klong Wang Hip, Nakon Si Thammarat); *ibid.*, vol. 2, June, 1916, p. 52; Bull. Raffles Mus., No. 3, 1930, p. 21; Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, p. 290; Hennig, Temminckia, vol. 1, 1936, pp. 211-213, map 12.

Diagnosis: A moderately small species (to 85 mm. snout to vent); head small, nostril lateral, directed outward; tympanum scaly; a prominent scale on back part of supraciliary edge; wing-membranes of male usually orange with numerous spots; a blue spot on each side of base of dewlap.

Description of species (from No. 173, Na Bon Coffee Camp, Nakhon Si Thammarat): Head rather small; rostral three times as wide as high, bordered behind by five scales and laterally by two labials; nasals craterlike, directed outward and slightly upward, separated from rostral by two rows of scales; separated from each other by six rows; scales on top of head variable in size, shape, degree and character of rugosity; scales in canthal area on front part of supraorbital area, and on inner dorsal part of supraorbital area, largest; canthal scales continued on front half of supraciliary border, then, after a short break filled with small scales, a larger compressed tubercular scale on posterior part of supraciliary region; at posterior upper edge of orbit, a strong conical tubercular scale; occipital scales large, some strongly rugose.

Supralabials eight or nine, not keeled; a series of three en-

larged scales form a ridge behind eye, third compressed, elevated; tympanum covered with eight or ten small scales; mental with a labial border about equal to that of rostral; ten infralabials, last small; a small nuchal crest, low, indistinct, except for two or three larger compressed scales at beginning, behind occiput. A high tubercular scale a little above tympanum; scales on outer part of wattles enlarged, keeled, the keels directed downward and back-

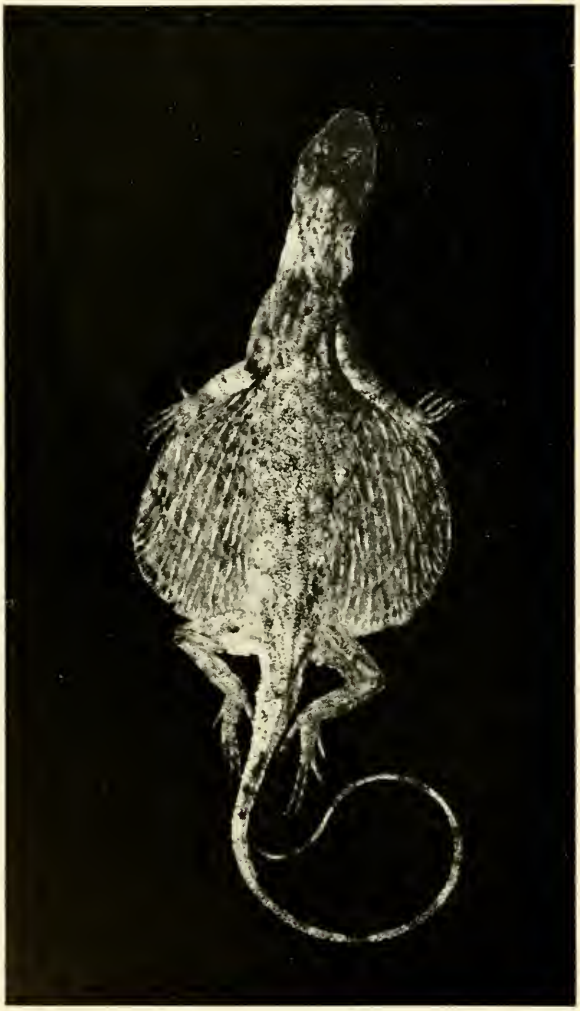


FIG. 34.—*Draco maculatus maculatus* (Gray). Khao Chong Forest Experiment Station, Trang province, Thailand. Actual length, 190 mm.

ward. Dewlap of male large (26 mm.), much longer than head (18 mm.), the terminus moderately attenuate, and covered with somewhat enlarged scales on anterior edge; scales on back moderately large, a little smaller on sides. Ventral scales a little larger than dorsals and strongly keeled. A spaced row of large tubercular scales at base of wing-membranes; wing-membranes moderately large; tail with a median dorsal serrate crest highest somewhat behind base; postfemoral fringe of scales rather weakly developed, as are lateral caudal scales; leg does not reach elbow of adpressed arm; five ribs support wing-membranes.

Color in life: Wing-membranes above orange to orange red; very fine indefinite parallel lines of pinkish yellow growing yellowish cream near body follow lines of slightly enlarged granules of wing; black spots covering wing tending to form five or six transverse curving series and at the same time spots (unequal in size) tend to form slightly diagonal parallel rows running from body to near periphery of wings; arms and legs indefinitely marked; digits distinctly banded; twelve rather darker bands surrounding tail; five discrete black spots on neck with a broad chevron-shaped band across shoulders; chin covered with fine black punctations; a bright-blue spot on each side of base of dewlap, the latter with front, sides and terminal parts pearl-gray; under parts yellow; yellowish or yellowish white under lappets; undersurface of wing-membranes magenta with two or three black spots on outer part; venter dirty white with greenish reflections and some minute blackish dots.

Measurements in mm.: Snout to vent, 87; tail, 138; total length, 225; snout to arm-insertion, 28.5; axilla to groin, 46; head length, 18; head width, 11.5; length of dewlap, 26; wingspread, 76.

Variation: The variation is considerable in this form. At Na Bon, in a small lot of coconuts, there was a population that had bright yellow-orange wings, only the proximal parts being covered with small black dots, the black spots on the outer under periphery large. The nuchal markings are dim or absent. The front of the head is dark with a gray frontal mark and a broken gray band across back part of the orbit. The males and females are colored alike. The largest of several specimens is 74 mm. snout to vent. While there was no typical Y-shaped frontal series of scales, a group of large keeled scales formed a V-shaped series (this area has perhaps suffered an injury in the described specimen and the series is incom-

plete); however several specimens do show a poorly defined or well-defined Y-shaped series.

Distribution: The limits of the range of the typical form of *Draco maculatus maculatus* is difficult to define. The specimen described is from an elevation in the mountains of about 300 to 400 meters and is relatively close to the type locality (Penang, Malaya ± 200 km.).

Draco maculatus divergens Taylor

FIG. 35

Draco divergens Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, June 13, 1934, pp. 291-292, pl. 17, fig. 4 (type-locality Doi Suthep Mountain, Chiang Mai; the original locality was given only as Chiang Mai, the Doi is some 5 kilometers from the city, and it was here at an unknown elevation that the specimen was taken).

Draco maculatus: Taylor, *ibid.*, p. 290.

Diagnosis: A small draco, characterized by having nostrils lateral, but directed somewhat upwards; tympanum concealed by scales; a compressed spine in the posterior superciliary edge; a pair of prominent conical scales at upper posterior corner of the orbit; a prominent nuchal crest composed of small scales (about 25) the two or three anterior more prominent than others; gular appendage narrow, lanceolate, terminating in a greatly attenuated point, covered with large, strongly imbricated scales. Arm extended forward tips of fingers reach beyond snout; leg extended, toes reach axilla. Grayish mottled darker above; wings pinkish, with dim spots and lines; below large scattered dark spots; gular appendage dark; somewhat greenish orange at base with two small blue spots not extending onto lateral nuchal appendage. Row of enlarged scales behind shoulder.

Description of species: Head moderately large, distance from tip of snout to orbit very slightly less than length of orbit; lateral profile from top of orbit to rostral nearly a straight line, slightly broken in region of forehead by a slightly raised area on forehead; rostral large, smooth, twice as wide as high, bordered by seven scales. Nostrils lateral, directed outwards and upwards, separated from rostral and first labial by a single scalerow, from each other by six rows; rostrum constricted behind nostrils; loreal region concave; labial region forming a broad shelf; a double row of keeled or trihedral scales from nostril to orbit; anterior supraciliary border with one large keeled scale followed by three (or two) keeled scales, the keels directed outward; three larger keeled scales on snout form a

longitudinal row which joins mesially a curved transverse subconical or keeled series extending from anterior face of supraorbital region across forehead; a group of scales on supraorbital region enlarged; scales in occipital region larger than other head scales, consisting of a median group of five flanked on each side by a group of five somewhat larger scales, somewhat rugose or trihedrally keeled; posterior supraciliary edge with a compressed spinelike scale; posterior border of orbit with a pair of bluntly conical scales;

FIG. 35.—*Draco maculatus divergens* Taylor. From Taylor, Acad. Nat. Sci. Philadelphia, vol. 86, 1934, pl. 17, fig. 4.

a group of postorbital scales from orbit to above anterior edge of tympanic region; posterior scale subconical; another prominent conical spine directly below this, and another larger, conical scale preceded by a smaller scale directly behind it, the three forming a triangle including tympanic area. Series of enlarged, distantly spaced scales begin on sides of neck, and continue to base of tail, along base of wing-membrane, scales more numerous and smaller anteriorly; scales on lateral gular appendage larger than dorsal scales, and strongly keeled; on either side of back behind shoulders a row of distant keeled scales terminating before reaching the middle of body. Scales on the back smooth or weakly keeled; wing membranes with numerous diagonal rows of larger scales separated by wider areas of minute scales; crest at dorsal surface of tail low; lateral fringe on base of tail prominent; posterodorsal side of femur with a few groups of larger keeled scales, and a prominent posterior femoral fringe continuous with a fringe on lower part of leg; ventral scales smaller than larger dorsals.

Upper labials 10-11; the row of scales bordering them above only slightly enlarged; nine lower labials, mental less than twice as wide as long, bordered behind by five scales. The gular appendage is elongate, more than once and one-half times the length of head, lanceolate, terminating in a sharp point, covered over most of its surface with enlarged imbricating scales. The posterior edge of gular appendage, instead of presenting a straight edge, tends to form a folded-in pocket at base, and when evaginated forms a pouch-like sack. No nuchal fold.

Color: Above variegated bluish gray with darker markings; a darker area on snout; darker lines on top of head enclose rounded areas in supraocular region; a dim mark borders parietal region, and one across temporal region; nuchal crest brownish, forming a shaft for a deep black arrow-shaped mark on middle of neck; a deep black line across shoulders and indefinite darker markings on back; tail indefinitely banded with lighter; limbs banded with somewhat darker marks; fingers and toes barred; wing-membranes somewhat salmon pink with scattered blackish dots on inner half of wing and very narrow lighter marks following enlarged scalerows; under surface with large spots of black, abdomen grayish; gular appendage dirty greenish, with a dim blue spot on either side of orange base; chin flecked with brown.

Measurements: Total length, 174 mm.; tail, 105 mm.; snout to vent, 69 mm.; foreleg, 30 mm.; hindleg, 37 mm.; axilla to groin,

36 mm.; head length, 17 mm.; head width, 11 mm.; snout to orbit, 5.2 mm.; orbit, 5.6 mm.; snout to foreleg, 24 mm.; gular appendage, 27 mm.

Remarks: Taylor *loc. cit.* has compared the species with *volans* incorrectly. The reason for this was the spotting under the wings (which in the type differs from the spotting in *maculatus maculatus*), and because of having at hand a northern Luzon specimen of what was identified as *volans*, with the tympanum covered with small scales. Occasionally specimens of *volans* from the Indo-Austrian Archipelago may have the tympanum covered with small scales.

A confusing factor is that in certain populations of *maculatus* both sexes may have the same general color pattern. In others the spots are in strongly defined transverse rows or bands, especially in females, and their appearance differs greatly from most males. My series of the various subspecies have been too small to determine the significance of this variation.

The second row of enlarged scales arising on the nuchal region and passing straight back is probably the most distinctive character of *divergens* for separating it from the typical form. This character is reported as being present in *m. whiteheadi* which may be easily separated from other subspecies by the dewlap, blue at tip, and red at base.

Distribution: The form is known from northwestern Thailand. Most of the specimens I have seen (8) are topotypes collected by Gordon Young or myself.

Draco maculatus haasei Boettger

FIG. 36

Draco haasei Boettger, Zool. Anz., no. 433, 1893, p. 429 (type-locality, "Pratchedi," Khao Sebab; Chanthaburi province, Thailand); Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, pp. 288-289; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1088-1089.

Draco maculatus haasei: M. Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, 1915, pp. 239-240; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 4, no. 2, Mar. 1921, pp. 93-94 (Pulo Condore).

Draco maculatus: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 138-140 (*part.*).

Diagnosis: Related to *Draco maculatus maculatus* but differing chiefly in lacking a blue spot at the base of the dewlap; smaller size; scales on the wattles proportionally larger than in *maculatus;* base of gular appendage deep orange, without blue spots.

Description of species (from type-description): Head small; snout a little longer than diameter of orbit; nostril lateral, directed

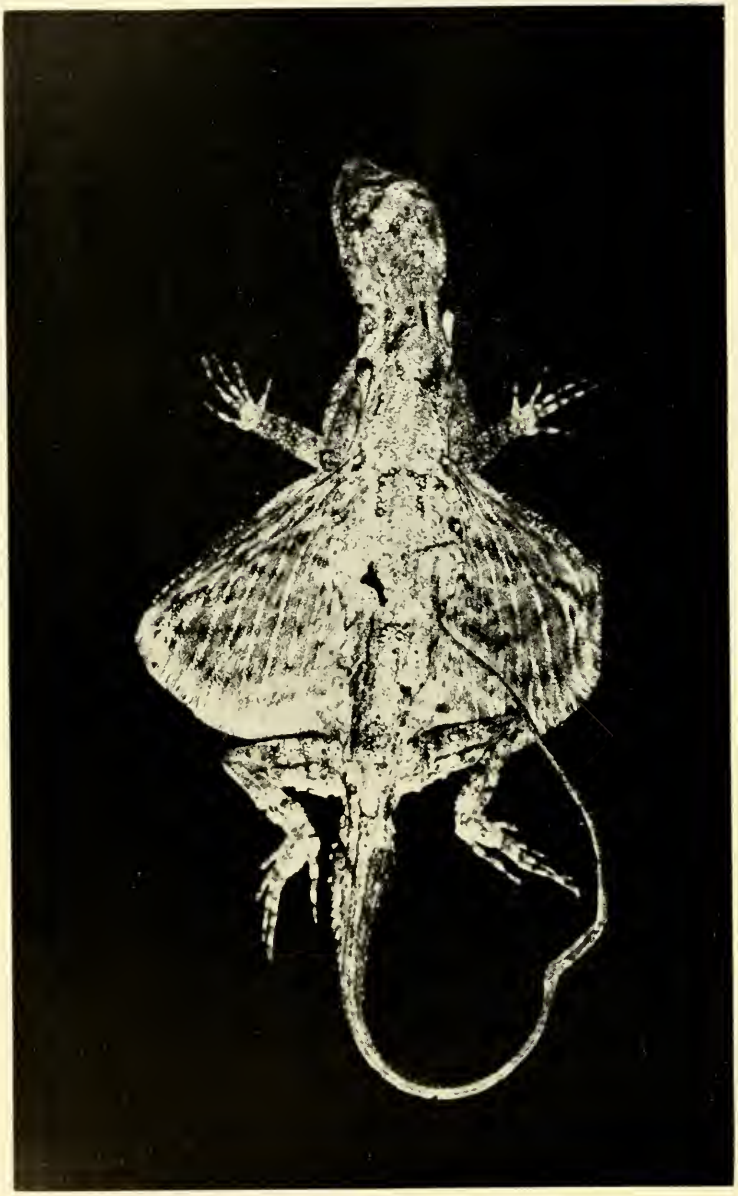


FIG. 36.—*Draco maculatus haasei* Boettger. No. 759, Sanoi River Forestry Station, Ubon province. Total length, 162; snout to vent, 64 mm.

outwards; tympanum scaled; upper head scales large, weakly keeled; a pair of scales on supraocular region distinctly enlarged, much larger than supralabials; a distinct compressed or conical scale at beginning of last third of supraciliary arch and a second broader and shorter one at end of supraciliary region; eight supralabials; gular appendage of male long, nearly twice head length, covered with scales which are somewhat larger than the ventral scales; upper side of lateral nuchal expansions covered with very large, strongly keeled scales, larger than supralabials and largest back scales. A very short and low nuchal crest consisting of eight scales; scales of back irregular, of very dissimilar form and size, largest reaching twice size of sharply keeled ventral scales, and with obsolescent keels or lacking keels altogether. On each side of the back and especially distinct in posterior part, a row of large trihedral keeled scales separated rather widely; arm laid forward reaches well beyond tip of snout; hind leg reaches axilla.

Color: Above coppery-red with metallic reflections and marked with blackish dots, those on neck arranged symmetrically; triangular black interorbital spot; wing membrane delicate orange with whitish longitudinal lines and on proximal half, richly strewn with small round black spots. Underside unicolor and only on anterior point of wing-membrane one or two black spots. Underside of head with brownish reticulation; underside of wattles deep orange lacking dark spots.

Measurements in mm.: Snout to vent, 65; tail, 113; total length, 178; head length, 14; head width, 11; arm, 28; leg, 38; dewlap, 23.

Distribution: Specimens of this subspecies have been taken near the type-locality on Khao Sebab, province of Chanthaburi, at an elevation of about 100 meters. I have also taken it near the city of Ubol.

It is quite probable that the form occurs in Cambodia since the type-locality is close to the Cambodian border.

Draco maculatus whiteheadi Boulenger

Fig. 37

Draco whiteheadi Boulenger, Proc. Zool. Soc. London, Nov. 1899, pp. 956-957, pl. 66, fig. 1 (type-locality, Hainan I.); M. Smith, The fauna of British India, Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 140 (Northern Siam); Hennig, Temminckia, vol. 1, 1936, p. 213-214; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1086-1088.

Diagnosis: Nostril directed laterally; tympanum scaled. Head small, snout longer than diameter of orbit; dorsal scales obtusely

keeled. Similar to *m. maculatus* but "snout longer and coloration different." The dewlap blue at end, red behind its base; wing-membranes brick-red above with small round black spots; colorless and unspotted beneath.

Description of subspecies: Head short, snout slightly shorter than diameter of orbit; rostral less than twice as long as wide, with eight glandular pits on front surface, bordered by two labials and five other scales; nasals craterlike the nostril directed outward, separated from rostral and labials by one row of scales; five or six scalerows separate nasals, snout constricted behind nasals; a Y-shaped series of scales on snout, basal part consisting of two large keeled scales, and the arms of two or three enlarged keeled scales reaching outwards and backwards; supraorbital areas outlined by semicircular series of enlarged irregularly keeled scales separated mesially by three longitudinal series; outer row of supraoculars very large, keeled; one (or two) large keeled supraciliary scales extending half length of supraciliary border; on middle of latter half of border, a compressed triangular scale, and at posterior border a large compressed tubercular one, flanked by one or two similar scales; six enlarged suboculars more or less continuous with a short series of three pyramidal scales, last two largest; two or three irregular canthals; nine loreal series; supralabials ten, all with two to four pits; an enlarged triangular tubercle between scaled tympanum and angle of mouth; twin tubercles some distance back of tympanum, and another pair above and slightly posterior to tympanum; "occipital" scale narrow, elongate, flanked by groups of five enlarged irregular scales on each side; distal to each of the two groups and slightly posterior a somewhat elevated group of about six irregularly enlarged scales, separated from each other by four small or two enlarged scales; on nape at normal point for the beginning of a nuchal crest two conical scales surrounded by eight scales, altogether forming a rosette. Infralabials 8-8, also bearing pits; mental unpitted its border about equal to rostral border, touched behind by two labials and five scales; gular scales minute; male gular appendage (21 mm.) longer than head (14 mm.), covered on its distal half by large regular scales; lateral nuchal expansions relatively small with larger scales above.

Nuchal crest not or barely indicated; a series of large somewhat compressed pyramidal or trihedral scales begins on neck and curves above arm, then follows along base of wing-membrane

to level of thighs, about 16 on neck anterior to wing, ten or eleven along wing-base; a short indefinite row of similar scales higher up on shoulders; scales of dorsal rows along back much larger than small ventral scales, keeled or smooth, often with their edges raised suggesting lateral keels. A distinct caudal crest; a series

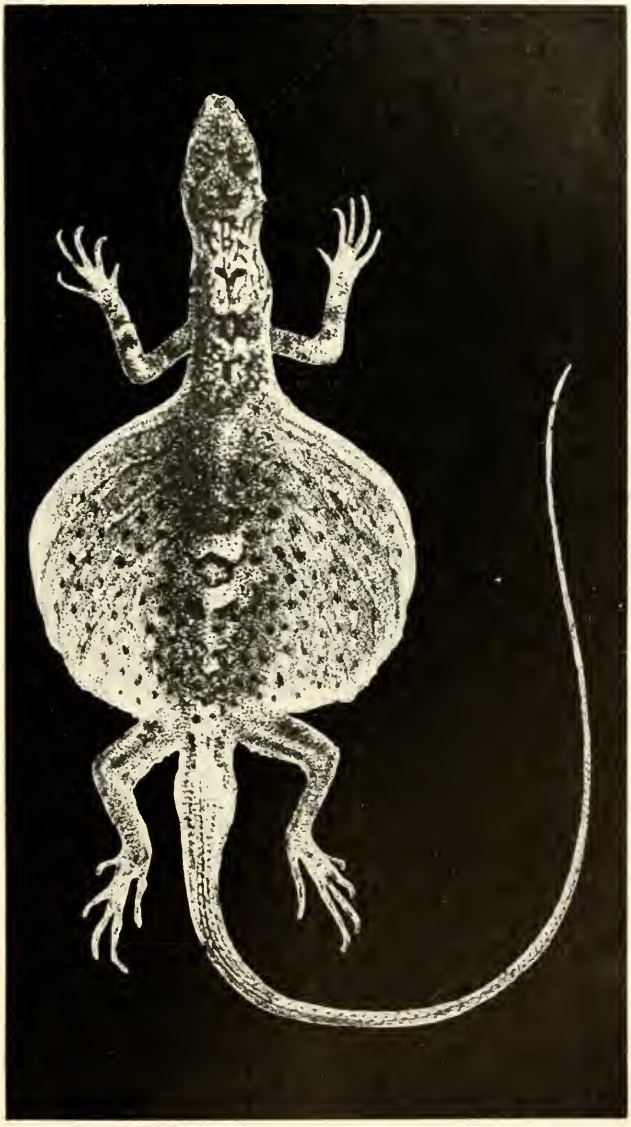


FIG. 37.—*Draco maculatus whitehcadi* Boulenger. From Boulenger, P. Z.S. 1899, p. 95-6, pl. 66, fig 1.

of mucronate scales begins on dorsal part of tail separated at first by three scalerows from caudal crest and more posteriorly comes to border the crest scales; another serrate series that begins on outer edge of base of tail comes later to border the two median ventral series, which have high keels. A fringe of enlarged scales along posterior edge of thigh; front dorsal part of thigh and tibia with enlarged keeled scales; 27 lamellae under fourth toe; scales on breast, on dorsal part of upper arm, and on dorsal part of forearm, enlarged, keeled; posterior edge of forearm with a fringe of larger scales.

Color in preservative: Above brownish, reticulated or dotted with some lighter marks, and with deep black marks on head and neck; wing-membranes light tan with black marbling or flecking, not forming bands or rows of spots; wing-membranes below immaculate gray save for a narrow elongate curved black mark near outer border. Chin darker, speckled with lighter; breast flecked with brownish spots; tail gray, banded with darker to tip; dewlap blackish on anterior margins, remainder whitish, probably orange-red in life; along side of the base of the dewlap are black marks separating the light color of underside of lateral nuchal expansions from that of dewlap area.

Measurements in mm.: Snout to vent, 64; tail, 102; length of head, 14; width of head, 10.5; height of head, 8.5; snout to orbit, 5; snout to tympanum, 12; axilla to groin, 33; arm, 27; leg, 33; length of gular appendage, 21; width of alar membrane, 22.

Remarks: Malcolm Smith (*loc. cit.*) has referred *D. whiteheadi* to the synonymy of *Draco maculatus* (Gray), but mentions the fact that specimens of this form occur in northern Thailand, Hainan and Tongking. The type is 86 mm. snout to vent, the tail, 148 mm.

Draco volans Linnaeus

This species, as reported by Hennig, *loc. cit.*, has four subspecies, only one of which occurs in continental Asia. Hennig has fixed the type-locality in Java, and believes the same form occurs throughout Thailand.

Draco volans volans Linnaeus

FIG. 38

Draco volans Linnaeus, Systema naturae, 10th Ed., vol. 1, 1785, p. 199 (type-locality, "India, Africa" restricted by Hennig (1935) to Java); Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 643; Günther, Reptiles of British India, 1864, p. 124; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 256; Proc. Zool. Soc. London, 1890, p. 3; Flower,

Proc. Zool. Soc. London, 1896, p. 868; *ibid.*, 1899, pp. 603, 636; Ridley, Journ. Straits Brit. Asiatic Soc., no. 32, 1899, p. 191; Laidlaw, Proc. Zool. Soc. London, 1901, vol. 1, p. 307; Volz, Zool. Jahrb. Syst., vol. 19, 1903-04, p. 421; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 57-58; Baumann, Zool. Jahrb., Syst., vol. 24, 1913, p. 259; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 3, Mar. 1915, p. 153 (Sai Yoke, Kanchanaburi); vol. 2, no. 2, Dec. 1916, p. 152 ("Tan Jong Mas, and Bangnara," Narathiwat province; and Nakhon Si Thammarat); M. Smith, Bull. Raffles Mus., no. 3, Apr. 1930, p. 21 (not found north of Nakhon Si Thammarat); Smedley, Bull. Raffles Mus., no. 6, 1931, p. 104; Brongersma, Zoolog. Meded., vol. 16, 1933, p. 22.

Draco volans volans: Mertens Abh. Senckenb. Naturf. Ges., 1930, p. 151; Hennig, Temminckia, vol. 1, 1936, pp. 176-179, map no. 2 (details of distribution).

Diagnosis: Small species, snout-to-vent length to 85 mm.; dewlap pointed, as long as, but rarely longer than head; males with nuchal crest; no median caudal crest; wing-membranes above, dark, with transverse darker bands indicated, enclosing lighter spots; bluish below with numerous black spots tending to form transverse bands; tympanum naked; an interorbital black spot; females with a black nuchal spot and usually punctate black spots on back. Wing membranes supported by six ribs.

Description of species (from No. 35722, Khao Chong Forest Experimental Station, Trang province): Head small. Rostral a little less than twice as wide as high, bordered behind by six scales and two labials; nasals lateral, rather small, craterlike, the nostril directed outward and backward; nasals separated from rostral by one or two scales, separated from each other by seven scales, anterior scale above nasal enlarged; snout about as long as orbit; a clearly defined inverted Y-shaped series of enlarged scales on forehead and snout; canthals with compressed edges not extending half way across supraciliary border; a blunt tubercle at posterior edge of supraciliary border, followed by a compressed spine; a pair of blunt tubercles in occipital region separated by three scales; scales on head keeled and somewhat corrugated; three enlarged scales in a longitudinal row behind eye; a distinct nuchal crest, serrate anteriorly; spinelike scale directly above tympanum, and one above and somewhat behind it; tympanum naked; supralabials nine (ten), not keeled; infralabials ten; mental small narrower than rostral bordered behind by two labials and three small scales; dewlap short, pointed, its length equal to head length or slightly longer; an indistinct row of enlarged widely separated keeled scales or groups of scales along base of wing-membranes, dorsally; a fringe of enlarged compressed scales bordering back edge of femur and tibia; dorsal scales of back irregular, some more or less keeled; venter

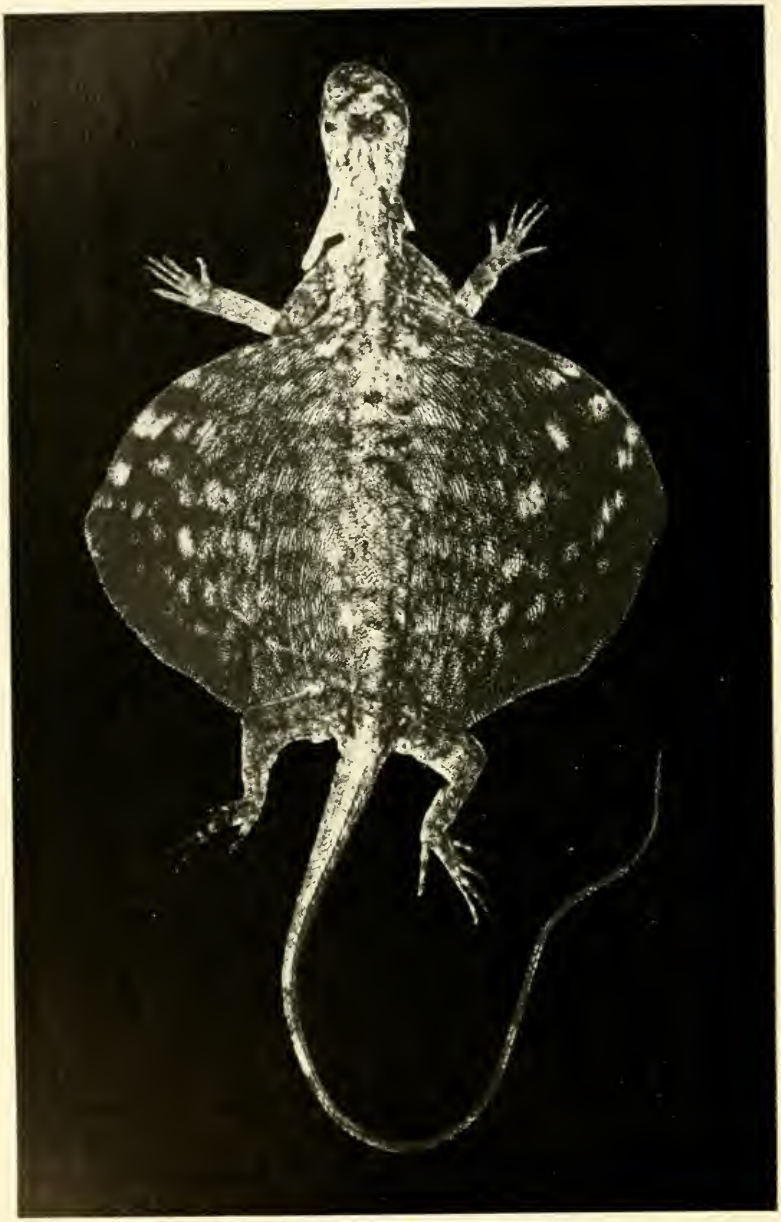


FIG. 38.—*Draco volans volans* Linnaeus. No. 34849, Bhetong, Yala, Thailand. Actual total length, 194 mm.

with keeled scales; no caudal crest. Arm reaching beyond snout-tip; leg reaching elbow.

Color in life: Variegated bronze-brown, olive, black and fawn above with some metallic irridescence; a black interorbital spot with two indefinite dark marks behind orbits; side of head fawn with darker flecks and reticulations; cream-stripe below eye extending onto and nearly across chin; bluish to ultramarine on neck, base of dewlap and underside of wattles; breast and venter bluish, lateral areas with numerous small black flecks the size of single scales. Wing-membranes brown, outer posterior parts black, enclosing lighter brown spots; underside of wing ultramarine with numerous black spots tending to form transverse rows; tail very indefinitely banded; bluish under arms and legs. Dewlap ultramarine at base, distal parts yellowish to flesh-color.

Measurements of *Draco volans volans*

NUMBER	35722	34849	35725	35726
Sex	♂	♂	♀	
Snout to vent	82	77	77	80
Tail	126	117	116	126
Snout to arm-insertion	27	24	24	28
Axilla to groin	47	48	43	49
Head length	18	16	17.5	19
Head width	10.9	10.2	10	11
Arm	28	25	25	28
Leg	32	30	30	30.6

Variation: There is considerable variation in the color of the region about the dewlap. Some specimens have the basal part greenish yellow which may become bluish in fixative; or it may be nearly clay white; there may be a slight greenish wash under lappets. The black flecks (size of one scale) are often arranged together in rows producing a reticulation. Occasionally the breast is bronze in color.

The wing is largely black enclosing brown spots, or distally yellowish-cream or grayish-white spots. The Y-shaped scale series on the snout is presumably always present.

The banding of the tail may be very clearly defined, in some specimens, or scarcely discernible in others.

Distribution: The species is widely distributed in peninsular Thailand. It is known from the following provinces: Narathiwat,

Trang, Nakhon Si Thammarat, and north of the peninsula in Kanchanaburi. It extends into Malaya, the Malayan Archipelago, and reaches as far as Palawan in the Philippines.

Remarks: In 1915 Dr. M. Smith reported *volans* in Sai Yoke district, Kanchanaburi province. In 1930 he states that it does not occur north of Nakhon Si Thammarat. It is possible he changed his opinion as to the identity of the specimen, Sai Yoke being several hundred kilometers north of the southern locality.

Draco fimbriatus fimbriatus Kuhl

FIG. 39

Draco fimbriatus Kuhl, Beitr. Zool. vergl. Anat., 1820, p. 101 (type-locality "in India orientale" restricted to the Malay Peninsula by Hennig); Fitzinger, Neue Classification Rept. Wien., 1826, p. 48; Flower, Proc. Zool. Soc. London, 1899, p. 636; Lidth de Jeude, Notes Leyden Mus., 1904-05, vol. 25, p. 190; Günther, The reptiles of British India, 1864, p. 123; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 265; Fasciculi Malayenses Zool., vol. 1, 1903, p. 151; Journ. Federated Malay States Mus., vol. 3, 1908, p. 64; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 59; de Rooij, The reptiles of the Indo-Australian Archipelago, vol. I, 1915, p. 79, 80; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916, p. 52; Journ. Federated Malay States Mus., vol. 10, 1922, p. 268 (Gunong Tahan, Malaya); Journ. Nat. Hist. Soc. Siam, vol. 2, no. 2, Dec. 1916, pp. 151-153; Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, pp. 289-290 (?Chantaboon = Chanthaburi, Chanthaburi. There is a possibility that this specimen is from a locality other than the one on its label). Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 58, pt. 2, 1958, p. 1084. (The statement "Reported by Taylor (1934) from Chiang Mai," should read "from Chanthaburi.")

Draco (*Rhacodracon*) *fimbriatus:* Fitzinger, Systema reptilium, 1843, p. 50.

Draco fimbriatus fimbriatus: Hennig, Temminckia, vol. 1, 1936, pp. 202-203.

Diagnosis: A large *Draco* with a wingspread of 125 mm.; snout to vent length, 116; tail, 191; male wattles and dewlap saffron to salmon in color with some indefinite radiating lines of gray; underside of wings gray with rather large spots chiefly on distal portions; male only with a distinct nuchal and caudal crest; an inverted Y-shaped series of scales more or less in evidence on snout; nostril directed outward; tympanum naked.

Description of species (from No. 234, Na Bon, Nakhon Si Thammarat): Head large (19 mm. wide, 26 mm. long); diameter of orbit (8 mm.), shorter than snout length (10.5 mm.); a series of three large scales form a median row on snout but branches forming the "Y" are indicated by a single enlarged scale near elevation of orbit (other specimens with the Y-shaped series complete or nearly so); rostral nearly three times as wide as high, bordered behind by two labials and eight postrostral scales; rostral separated from craterlike nasals by two rows of scales; twelve rows of scales be-

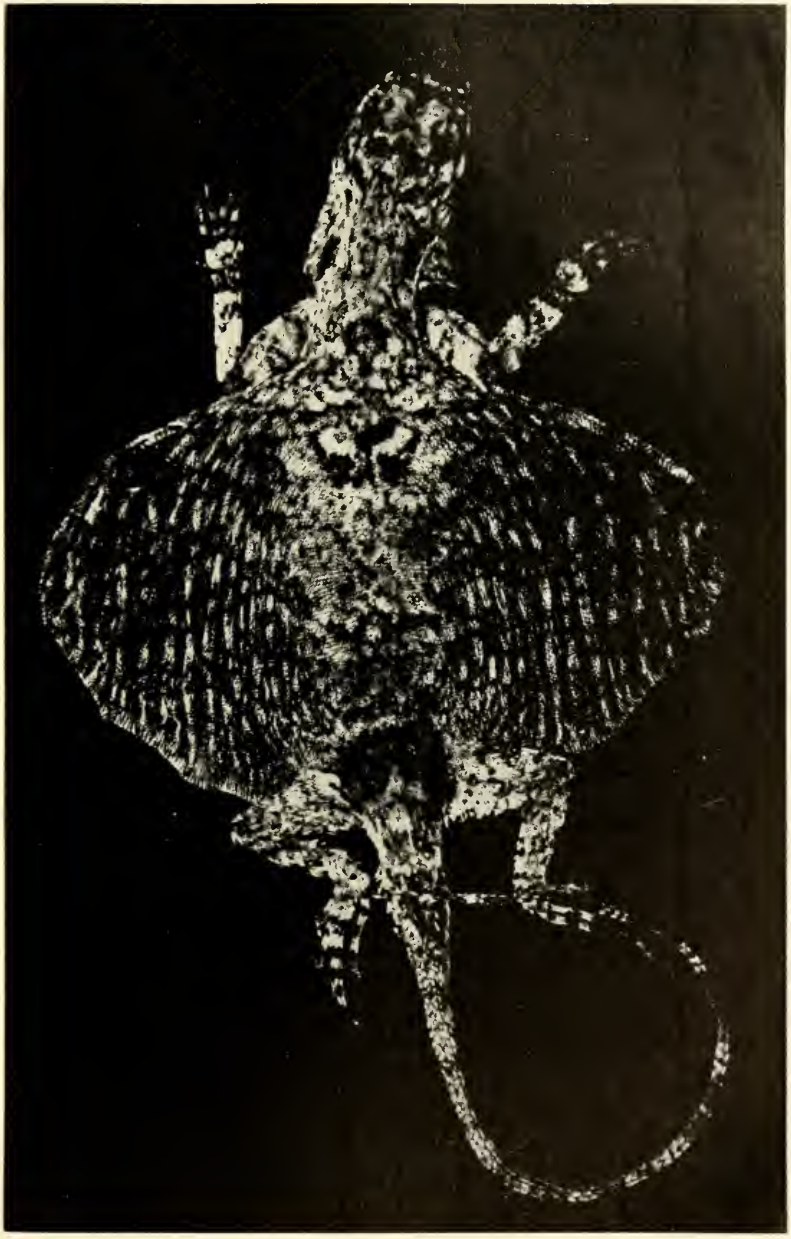


FIG. 39—*Draco fimbriatus fimbriatus Kuhl.* No. 34431, Na Pradoo, (Bukit Besar, near waterfall), Pattani province, Thailand. Actual length, 235 mm.

tween nasals; three or four enlarged canthals, last two above edge of orbit; a pair of blunt spines on each side above back edge of orbit; two groups of enlarged scales on occiput; a nuchal crest extending back to beginning of shoulders, anteriorly elevated, with four or five scalerows on side of crest; tympanum distinct; an irregular row of conical scales above tympanum, and a second row indicated; a much enlarged scale above and anterior to tympanum; supralabials, 12-12; infralabials, 9-13; mental twice as wide as deep bordered by two labials and five small postmental scales; scattered enlarged scales in lower temporal region and on lower jaw, the scales light (cream) in color. Scales on top of head keeled and corrugated; dewlap elongate (35 mm.).

Scales on back rather uniform save for a series of scales in groups along dorsal wing-base, each usually composed of groups of three or four scales with a median one considerably the largest, the groups separated often by half a centimeter; fringe of scales on back of thigh; a well-defined crest beginning near base of tail and continued greater part of length, slight lateral fringe with two much enlarged scales near base. Tail laterally compressed. Scales on venter strongly keeled.

Color in life: Head brownish olive above with black punctations; above on body rich brown with indefinite bands of varying shades; a series of small punctate black spots on occiput, dorsum, and base of tail, most conspicuous of which are three pairs, one on occiput, one on nape, and one on shoulder. Wing-membranes above, grayish with indefinite subparallel gray lines; tail banded with brownish and gray near base, becoming clay and blackish more distally, the bands surrounding tail; limbs bronzy olive above, grayish or bluish white below; dewlap saffron, the color continuous with saffron of underside of wattles; breast and venter cream with very indefinite, darker punctations indicated; underside of wing-membranes gray (sometimes with a yellow wash and black spots larger and more numerous distally); base of tail white below; chin and part of side of head punctate with black and cream.

Variations: The female specimens differ from the males. No. 233 ♀ lacks the black dorsal punctations but instead has a frontal light band with an elongate black interorbital mark; two diagonal black marks on the back of the head; an elongate V-shaped mark and a diamond-shaped mark on shoulders; three more or less angulated spots with four darker lines on tail, the outer connecting with an indefinite dark line from dorsal wing base. The venter has a wash of saffron, stronger posteriorly.

Measurements of *Draco fimbriatus fimbriatus*

NUMBER*	234	174	455	233	165
Sex	♂	♂	♂	♀	♀
Snout to vent	112	112	99	114	117
Tail	181	145+	154	189	162+
Head width	18	17.8	16.1	18	19
Head length	24.2	23.5	19.8	26	25.6
Snout to arm insertion	38	37	34	39	39
Axilla to groin	60	59	49	62	64
Wingspread	117	114	98	124	112
Dewlap	35	38	33	21	20
Arm	44	45	40	45	44
Leg	48	50	44	51	54

* From, Na Bon Nakkon Si Thammarat.

The dewlap is small (16 mm.) with a slight saffron suffusion extending onto the underside of wattles. The wing-membranes resemble those of males.

No. 165 ♀ is very much darker above but the dorsal markings are very similar to the female, No. 233. The dewlap has no saffron but the dark gray longitudinal marks are visible; the underside of the arms are spotted black, and the yellowish venter is strongly marked with five black punctations. There is no nuchal or caudal crest in the female.

Distribution: The speceis is known in the southern part of Peninsular Thailand, specimens having been taken in Pattani, Nakhon Si Thammarat, and possibly in southeastern Thailand in Chanthaburi.

Elsewhere it is found in Malaya and in the larger and a few of the smaller islands of the Indo-Malayan group.

Remarks: The females have four eggs in the oviducts. These measure approximately 17 x 9.8 mm. They do not display an angular terminal shelf as is present in *D. blanfordii.*

Draco punctatus Boulenger

FIG. 40

Draco punctatus Boulenger, Ann. Mag. Nat. Hist., ser. 7, vol. 6, 1900, p. 189 (type-locality, Larut Hills, Perak, restricted); Fasciculi Malayenses . . . Zoology, vol. 1, 1903, p. 151, pl. 10, fig. 1; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore . . . Reptilia and Batrachia, 1912, pp. 59-60; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916, p. 53 ("Patani"); *ibid.*, vol. 2, no. 2, Dec. 1916, p. 153 near sea level, "Bangnara, Patani" = Narathiwat, Narathiwat, Thailand); Bull. Raffles Mus., no. 3, 1930, p. 21; Hennig, Temminckia, vol. 1, 1936, pp. 182-183.

Diagnosis: Medium large species, 91 mm. snout to vent; head relatively large; snout as long as diameter of orbit; nostril lateral directed outwards and somewhat upwards; male dewlap a little shorter than head; very distinct nuchal and caudal crests, latter with pointed scales; inverted Y-shaped series of scales on forehead and snout. Grayish with rusty red on top of head and along middle of back; head and back with numerous black dots; membranes of wings black above streaked with whitish; grayish white on underside; dewlap and underside of wattles, chrome-yellow. Six ribs in wings.

Description of species (from No. 35744, Khao Chong, Trang): Head large with a clearly defined, inverted, Y-shaped, series of enlarged keeled scales on frontal region (and snout); rostral about three times as wide as high, bordered laterally by two labials and posteriorly by five or six postrostral scales; nasals large, craterlike, nostrils directed outwards, somewhat upwards and backwards, separated from each other by six scalerows, from rostral by a single scale; snout constricted somewhat behind nostrils; canthal scales compressed and keeled, the series continued backwards to middle of supraciliary border; a moundlike scale at posterior point on supraciliary border, preceded after an interval by an enlarged compressed scale; head scales rugose or keeled, variable in size, those on inner part of supraocular regions and on sides of occiput largest; two or three enlarged scales in a longitudinal row behind eye; tympanum naked with one large compressed scale above, and one behind; supralabials nine or ten with an enlarged scale lying above last; infralabials ten (injured on left side); mental rectangular, labial border about equal to that of rostral, and followed by two labials and five postmental scales; gular dewlap triangular not quite as long as head. A strongly developed nuchal crest; a row of enlarged scales at base of wing-membranes along upper side of body, these scales (or groups of scales) separated by intervals; five ribs support wing-membranes; dorsal scales of body smooth, largest near mid-line, about as large as heavily keeled ventrals. Tail with a strong crest, the crest scales alternating larger and smaller, continued for most of tail-length; a fringe of compressed scales on back of thigh and tibia only moderately developed.

Color: Above greenish with rusty red or brown on top of head and at points on neck, shoulders and back; head on top, side and underside, and dorsal surface of back with punctate black dots of varying size; limbs spotted or banded above; tail with bands of

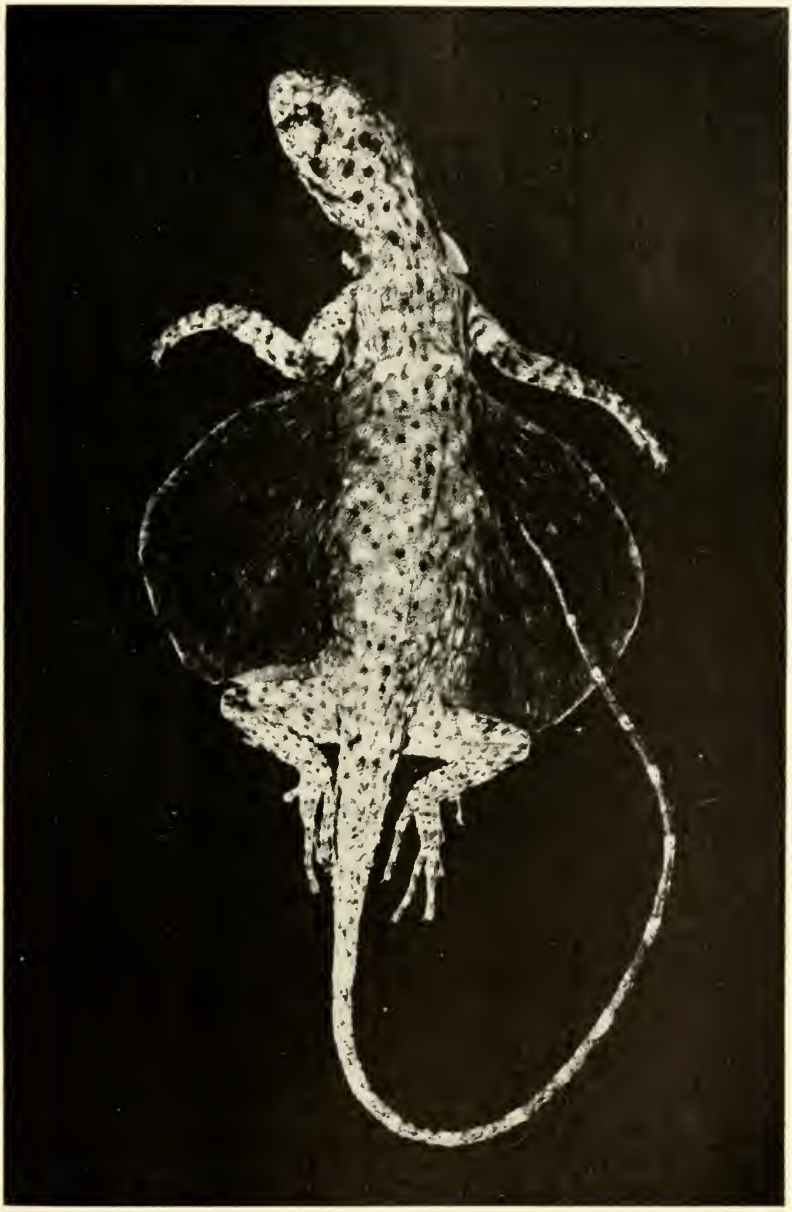


FIG. 40.—*Draco punctatus* Boulenger. No. 35744 Khao Chong Forest Experiment Station, Trang province, Thailand. Actual length, 227 mm.

lighter and dark gray; wings black with fine broken gray streaks tending to parallel body when wings are folded; undersides of wings gray-white to slightly ultramarine without black spots; breast and venter bluish; chin with black and white dots, dewlap and underside of nuchal lappets chrome-yellow (fading to cream-white).

Measurements in mm.: Snout to vent, 84; tail, 143; snout to arm-insertion, 30.6; axilla to groin, 46; head-width, 12.8; head-length, 20.6; wing-spread, 73; arm, 37; leg, 44.

Distribution: This species is rare in collections. In Thailand it has been taken once at "Bukit Besar," Pattani, at an altitude of 2500 ft. So far as I know the specimen from Khao Chong, Trang, is the second known from Thailand. It is doubtless confined to the provinces of southern Thailand.

Outside of Thailand it has been taken in the Larut Hills of Perak, Malaya, and in Borneo.

Remarks: Boulenger states that the tympanum of the type is nearly as large as the eye-opening; that there are ten or eleven supralabials, the dorsal head scales unequal, keeled, the leg reaching to axilla or between axilla and elbow of arm. The color is described as dark gray above, with a paler reddish ventebral stripe; back and head above and beneath, with large black dots; wing membranes black above, throat and belly pale blue; inner side of neck-lappets and extremity of gular appendage lemon yellow.

A Bornean specimen was included with the type. Hennig, *loc. cit.*, however, restricts the type-locality to Larut Hills, Penang.

Draco quinquefasciatus Hardwicke and Gray

Two forms of this species are recognized. The type-locality of the typical form is Penang, Malaya. The other subspecies is Bornean. Only the former occurs in Thai territory.

Draco quinquefasciatus quinquefasciatus Hardwicke and Gray

FIG. 41

Draco quinquefasciatus Hardwicke and Gray, Zoological Journ., vol. 3, 1827, p. 219 (type-locality, Penang, Malaya); Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9, Syn., 1831, p. 59; Günther, The reptiles of British India, 1864, p. 126; Flower, Proc. Zool. Soc. London, 1899, p. 637; Boulenger, Ann. Mag. Nat. Hist., ser. 6, vol. 8, 1891, p. 288; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 63 (Trang Thailand); de Rooji, The reptiles of the Indo-Australian Archipelago, vol. 1, 1915, pp. 81-82 (Sumatra, Borneo, Malacca, Penang); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June, 1916, p. 53; *ibid.*, vol. 2, no. 2, Dec. 1916, p. 154 (Tanjong Mas and "Bangnara" = [Narathiwat]); Bull. Raffles Mus., no. 3, 1930, p. 23.

Draco quinquefasciatus quinquefasciatus: Hennig, Temminckia, vol. 1, 1936, pp. 192-193.

Diagnosis: A large form, 105 mm., snout to vent; head relatively small; tympanum concealed, nostril directed upwards; a slight nuchal fold; no caudal crest; upper head scales small, subequal; dewlap narrow, reddish brown, dotted with darker; wings red, with five curved black bands of varying width, as broad as interspaces;

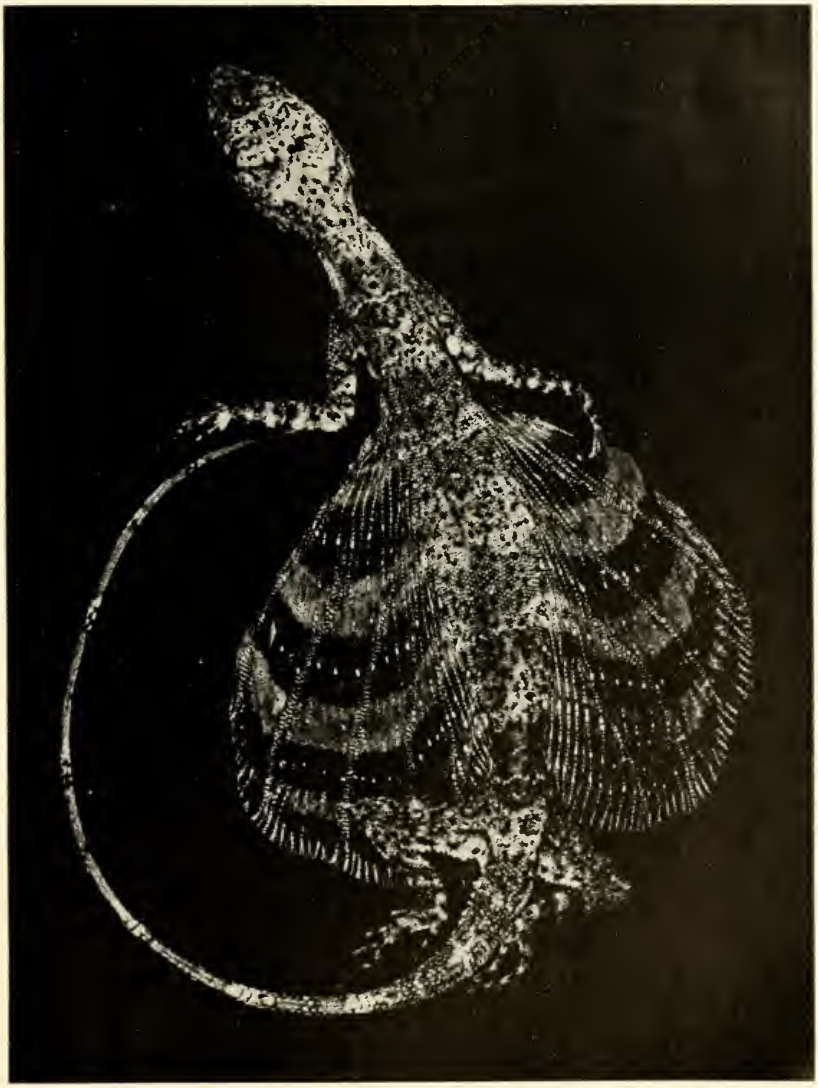


FIG. 41.—*Draco quinquefasciatus quinquefasciatus* Hardwicke and Gray. EHT-HMS No. M190♀. Ulu Langat Forest Reserve, Kajang, Selangor, Malaya. Actual length, snout to vent, 102; total length, 262 mm.

on underside of wings usually much narrower black bands; a black band across neck.

Description of species (from EHT-HMS No. M194). Head moderate in size, snout about length of orbit; rostral about two and a half times as wide as high, the upper edge denticulate, its surface rough with slight vertical striations; bordered laterally by two supralabials and posteriorly by nine postrostrals; nasal craterlike, nostril directed upwards and slightly backwards, separated from rostral by two scales, separated from its fellow by six scalerows; posterior canthals distinguishable, intermingled with anterior supraciliaries; supraciliaries bordered by tiny undifferentiated scales; tympanum completely concealed by small scales; 14-15 supralabials, last one very small, each with an indistinct keel and a ridge across lower side; mental triangular, with a labial border about equal to that of rostral; 15-16 infralabials, last very small, each with a longitudinal ridge at upper edge and a dim keel; mental bordered by a pair of chinshields the first of a series of six or seven larger scales; lappets on side of neck small; dewlap of female bearing a small, very slender terminal part; that of male much larger, reaching a length of 12 mm.; scales on snout irregularly conical, elevated, more or less keeled; a median series of slightly larger scales longitudinally keeled, scales not forming a Y-shaped pattern; scales above eyes, more flattened, keeled, imbricating; scales along supraciliary border small and lacking an enlarged scale on posterior part. An indistinct longitudinal row of larger scales runs back from middle of the posterior border of orbit toward tympanic area; scales above lappets enlarged, a few keeled; dorsal scales not or rarely keeled, subcycloid, strongly imbricate; a spaced row of enlarged more or less keeled scales at base of upper wing-membranes, white in color; scales on venter strongly keeled, as large or larger than dorsals, keels directed inwards; caudal scales strongly keeled; two rows of subcaudal scales forming two elevated ridges with a lateral ridge bordering them; no median caudal crest in female; paired scales on median dorsal surface of tail, without trace of a crest in males.

Arms moderate, the wrist fails to reach beyond snout; leg barely reaches elbow of adpressed arm; wing membrane ample, supported by six ribs; fringe of free scales along back of thigh moderate, reduced on tibia.

Color: Above reddish brown, dotted with darker on head, neck and dorsal surface of body; wings red above with five continuous

black bands of solid black color save for a series of small whitish dots covering slightly enlarged scales along their middle; intervening red bands about same width and curvature; black bands vary in width, second widest, last narrowest; these bands dimly indicated across the posterior part of the body; tail banded with gray and brown; below a series of broken transverse black bands directly below upper dark bands, reddish color appearing below; chin and part of throat bluish gray flecked with light and dark; dewlap distally grayish brown; a black band crosses neck in front of dewlap.

Measurements of *Draco quinquefasciatus quinquefasciatus*

NUMBER	193	191	189	192	190	194
Sex	♂	♂	♂	♀	♀	♀
Snout to vent	95	94	101	99	101	101
Tail	166	125+	164	162	162	162
Snout to arm	30	28	33	30	32	31
Axilla to groin	55	55	60	55	59	59
Width of head	13	12	13	13	13	13
Length of head	18.3	18.6	19	19	20	21
Arm	35	35	39	35	38	39
Leg	42	40	44	43	45	46

Variation: In some specimens the body is traversed by darker bands of a width equivalent to that of the transverse wing-stripes and occasionally the intervening areas are somewhat reddish.

In M190 there is little or no reddish brown. The front of the head is black; the latter half of the interorbital area and occiput are bluish gray variegated, and bordered by a narrow dark line. A broad light band with irregular edges crosses back of occiput, bordered by black behind. There are two transverse brownish spots which may be edged with minute white flecks. There are brown and fine white flecks scattered over head and dorsum. The basal parts of the wing-membranes are less red than the outer parts.

Distribution: The reason for including this species in the fauna of Thailand is the capture of specimens at "Tanjong Mas and Bangnara," localities in Narathiwat. I have seen one other specimen, taken in Yala, and Boulenger (1912) reports it in Trang.

In Malaya it is widespread. It also occurs in Borneo.

Remarks: All the specimens measured are from Selangor, Malaya. I have not found specimens in Thailand.

Draco melanopogon Boulenger

FIG. 42

Draco melanopogon Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 3, 1887, p. 492 (type-locality, Malacca, Malaya); Günther, Novitates Zoologicae II, 1895, p. 499; Lindholm, Jahrb. Nass. Ver., vol. 54, 1901, pt. 1, p. 307; Volz, Zool. Jahrb., Syst., vol. 19, 1903, p. 421; Boulenger, Fasciculae Malayenses, Anthropological and Zoological results of an expedition to Perak and the Siamese Malay States, 1901-1902, Zoology, pt. 1, 1903, p. 152; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 62; de Rooij, The reptiles of the Indo-Austrialian Archipelago, vol. 1, Sauria, 1915, p. 84; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916, p. 53 (Nakhon Si Thammarat); *ibid.*, vol. 2, no. 2, Dec. 1916, p. 154; Journ. Federated Malay States Mus., vol. 10, 1922, p. 268; Bull. Raffles Mus., no. 3, 1930, p. 25; Hennig, Temminckia, vol. 1, 1936, pp. 207-209, map no. 10; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1093-1095 (Phatthalung Province; Ban Chawang, Nakhon Si Thammarat).

Diagnosis: Wingspread about 75 mm.; snout-to-vent length about 85 mm.; dewlap much longer than head, terminating in a dull point, coal black except for a triangular posterior area near base which is ultramarine, gray, or pure white; wing-membranes black with very numerous small yellow or yellowish-brown spots; back variegated green and olive; no caudal or nuchal crest; nostrils directed upward; no inverted Y-shaped series, or other enlarged scales on snout or frontal area. Coloration of females similar to males.

Description of species (from No. 203, taken at the Hydroelectric Dam near Na Bon): Head very short, diameter of orbit a third or more greater than length of snout; rostral four times as wide as high, rectangular, bordered behind by ten postrostral scales and two labials; nasals craterlike, directed upward and slightly backwards; a slight median longitudinal elevation on snout; inner supraocular areas with somewhat larger scales than frontal areas; occipital region with still larger irregular scales; a blunt tubercular scale at back edge of orbit, no tubercle preceding it; tympanum distinct; supralabials, 15-15; infralabials, 14-13; mental small, nearly hemispherical, bordered by two labials and six small scales; no spiny tubercles above tympanum or on neck; five widely spaced enlarged scales at base of wing membranes above; no nuchal crest; no caudal crest; small fringe of scales on back of thigh and at base of tail; dewlap elongate, terminating in a blunt point; leg reaching axilla.

Color in life: Head, back, base of tail, and limbs yellowish green, variegated, with some evidence of darker markings across back; arms and legs indistinctly barred with darker; wing membranes

above black with numerous yellow or greenish-yellow spots; near base of wings a series of longitudinal greenish subparallel lines. Chin greenish bronze anteriorly, followed by magenta with minute black flecks; dewlap black, much longer than head, the color extending under inner anterior part of wattles; back part of dewlap ultramarine, connecting with an area of ultramarine under wattles;

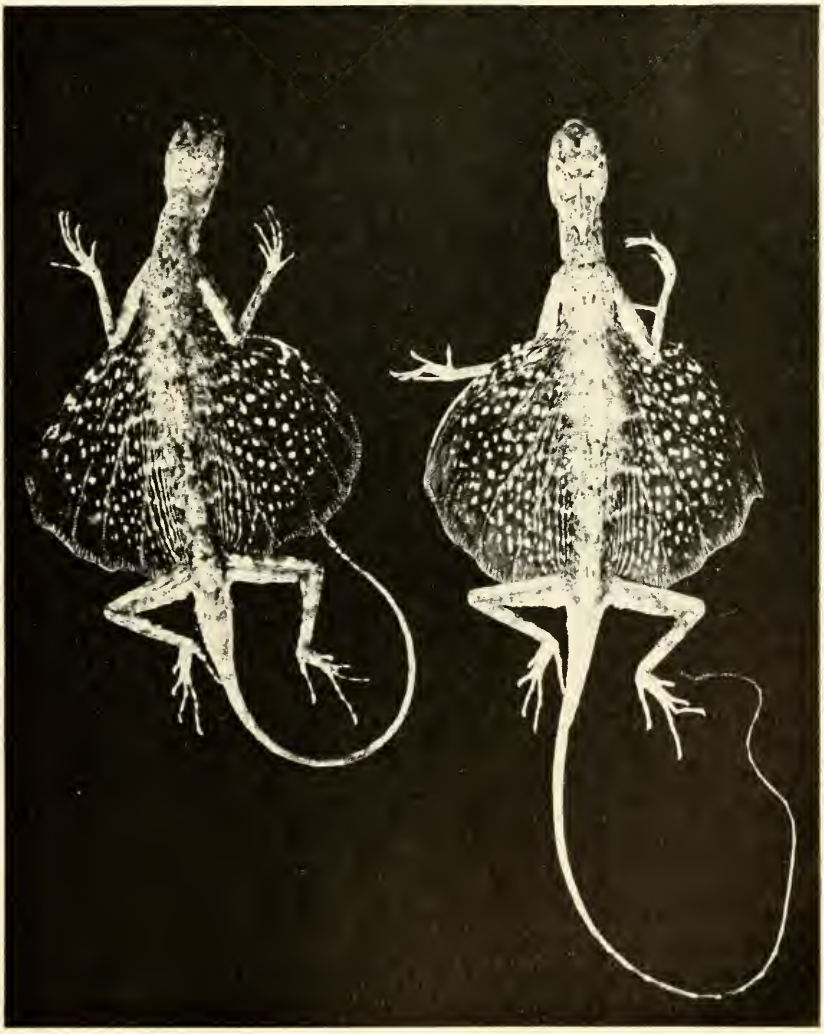


FIG. 42.—*Draco melanopogon* Boulenger. Left figure, No. 35743 ♂, Khao Chong (Mt.) Trang province, Thailand. Actual snout-vent length, 74 mm.; tail 144 mm. Right figure, No. 35625, Ronpibon, Nakhon Si Thammarat province, Thailand. Actual snout-vent length, 74 mm.; tail, 138 mm.

breast and venter dull yellow with reddish-brown flecks or spots; a thin greenish-yellow wash under wings, the black and yellow spots showing through; underside of arms and legs greenish yellow; tail banded with black and reddish brown, the brown becoming magenta on underside of tail. A bronzy area on back of head.

Measurements in mm. of *Draco melanopogon*

NUMBER*	200	203	204	205
Sex	♂	♂	♂	♂
Snout to vent	82	85	78	79
Tail	160	155	145	140
Snout to arm	24	24	24	24.5
Axilla to groin	46	43	42	44
Wingspread	77	75	74	71
Dewlap length	24	24	27	25.2
Head width	10.2	9.6	10.3	10.4
Head length	15	14	14	14
Arm	38	40	41	36
Leg	41	43	45	40

* Na Bon, Nakhon Si Thammarat

Variation: This species is strongly differentiated and is not apt to be mistaken for any other species. The males and females differ in the character of the dewlap, but in general coloration they are similar. The black on the dewlap is intense. The back part of dewlap, however, is somewhat variable; while always light, it may be gray, light ultramarine, or even pure white.

Distribution: In Thailand the species is seemingly found only south of the Isthmus of Kra. I have taken it in the provinces of Nakhon Si Thammarat, Yala, and Trang. It has been reported in Pattani and Phatthalung. It is not a rare species. The deep-black dewlap serves as a distinguishing mark that makes it easily identified in the forest.

Outside of Thailand the species occurs throughout Malaya. It is known also in Sumatra, Borneo, and the Natuna Islands.

Draco haematopogon haematopogon Boie, in Gray

Draco haematopogon Boie, in Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9; Syn. 1831, p. 39 (no type-locality given; fixed by Willi Hennig, Temminckia, vol. 1, 1936, p. 204, as "Malay Peninsula"); Schlegel, Abbildungen neuer oder unvollständig bekannter Amphibien . . . 1837-1844, p. 95, pl. 24, fig. 6; Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 14, p. 61; de Rooij, The reptiles of the Indo-Australian Archipelago, vol. 1, 1915, pp. 84-86.

Draco (Pleuropterus) haematopogon: Fitzinger, Systema reptilium, 1843, p. 51.

Draco microlepis Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 62 (*part.* Specimens from Larut Hills 3500 ft. altitude); Robinson and Kloss, Journ. Federated Malay States Mus., vol. 5, no. 3, Oct. 1914, p. 154 ("Koh Pennan"); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, p. 53 ("Koh Pennan"); Bull. Raffles Mus., no. 3, 1930, p. 23; de Rooij, The reptiles of the Indo-Australian Archipelago, vol. 1, 1915, pp. 84-86 (*part.*).

Draco haematopogon haematopogon: Hennig, Temminckia, vol. 1, 1931, pp. 204-206, map 9; Mertens, Treubia, vol. 24, part 1, Dec. 15, 1957, pp. 90-91, 101, 102.

Diagnosis: Nostril vertical; tympanum distinct not scaled; supralabials keeled; dewlap large in males, and one and one-half to two times length of head, covered with small scales; smooth dorsal scales smaller than ventrals; no nuchal crest; wing with five ribs.

The fixing of the type-locality of *Draco haematopogon* as the Malay Peninsula by Hennig eliminates the possibility of calling the species *microlepis* as has been done by previous authors, including Boulenger who described *microlepis* from Merabah, North Borneo and regarded specimens from the Larut Hills, Perak, 3500 ft., as being the same form.

Description of species (from literature): Head rather small; snout shorter or barely equal to height of head; nostril directed vertically upwards; head scales small, keeled; tympanum naked; supralabials 9-13, distinctly keeled; dewlap of male one and one-half to twice length of head, in female about two thirds as long as head; dewlap covered with small scales; dorsal scales smooth not larger than those on venter; no nuchal or caudal crests; wing supported by five ribs. Leg about one and one-half times the axilla to groin distance.

Color: Above usually greenish or grayish, the upper side of wing brick-red to reddish with some black spotting, the lower surface greenish, or gray without spots. Undersurface of body greenish; throat red, dotted with brown and with large black spot on each side of dewlap which is yellow in male (rarely whitish).

Measurements in mm. (of female from Java): Snout to vent, 95; tail, 132; head length, 16.5; head width, 12; axilla to groin, 36; dewlap, 11 (male, 24); leg, 53.

Variation: The tail length of the above measured specimen seems very small compared to 181 mm. recorded by de Rooij (*loc. cit.*) for a specimen having a snout-vent measurement of 91.

Distribution: In Thailand the species is recorded from Koh Pennan (Koh Pha Ngan) an island off the eastern coast of peninsular

Thailand. In Malaya the species is reported in the Larut Hills, Perak. It has been taken also in Java, Sumatra, and Borneo.

Draco taeniopterus Günther

This species, one having practically the same distribution as *D. m. maculatus*, has two recognized subspecies, the typical one and *t. indochinensis*. Only the former is known to occur in Thailand.

Draco taeniopterus taeniopterus Günther

FIG. 43

Draco taeniopterus Günther, Proc. Zool. Soc. London, 1861, p. 187 (type-locality, Chartaboum = Chanthaburi, Chanthaburi, Thailand); The reptiles of British India, 1864, p. 126, pl. 13, fig. E; Blanford, Journ. Asiat. Soc. Bengal, 1878, p. 125; Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 269; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 113; Flower, Proc. Zool. Soc. London, 1899, p. 637; de Rooij, The reptiles of the Indo-Australian Archipelago, vol. 1, 1915, p. 85; M. Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 4, Dec. 1915, p. 239; M. Smith, *ibid.*, vol. 2, 1916, p. 53 ("southeastern Siam; Dong Rek Mountains eastern Siam; Muang Song Forest, Prae northern Siam"); Bull. Raffles Mus., no. 3, 1930, p. 22; The fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 140-141.

Draco taeniopterus taeniopterus: Hennig, Temminckia, vol. 1, 1936, pp. 209-211, map no. 11.

Diagnosis: A small species, wingspread about 65 mm.; snout to vent, 76 mm.; nostrils directed upwards and backwards; distal part of dewlap rounded, covered with large translucent scales; olive to blackish-olive with a red to carmine area at base continuous with the carmine under wattles; wings olive, with four or five transverse dark bands; reddish or magenta on outer posterior part of wing; immaculate on underside, usually with a yellowish wash; two or three enlarged scales on snout in a line; more rarely an inverted Y-shaped scale-series on snout; no caudal crest. Little sexual dimorphism evident except in dewlap.

Description of species (from No. 457, Na Bon, Nakhon Si Thammarat): Head small, diameter of orbit greater than length of snout; rostral low, bordered behind by eight scales; nasals craterlike the nostril directed upwards and backwards, separated by five rows of scales; median longitudinal row of three enlarged scales on snout; four strongly keeled canthals; seven or eight supralabials; seven or eight infralabials; mental border on mouth shorter than rostral border; tympanum distinct; an enlarged rounded tubercle above tympanum, and a blunt tubercle back of orbital edge; scales on occiput enlarged, irregular in size, elevated; none or only a slight nuchal crest indicated; one or two enlarged scales in temporal

region; beginning on neck, a row of enlarged, widely-separated scales extends along basal part of wing-membranes, the enlarged scales often forming small groups; no caudal crest on mid-line; dewlap rounding behind, distinctly longer than head, greater part of its surface covered with enlarged pointed scales.

Color in life: Above, head dark olive with a dark band indicated between front of orbits (or a black median spot); a black border

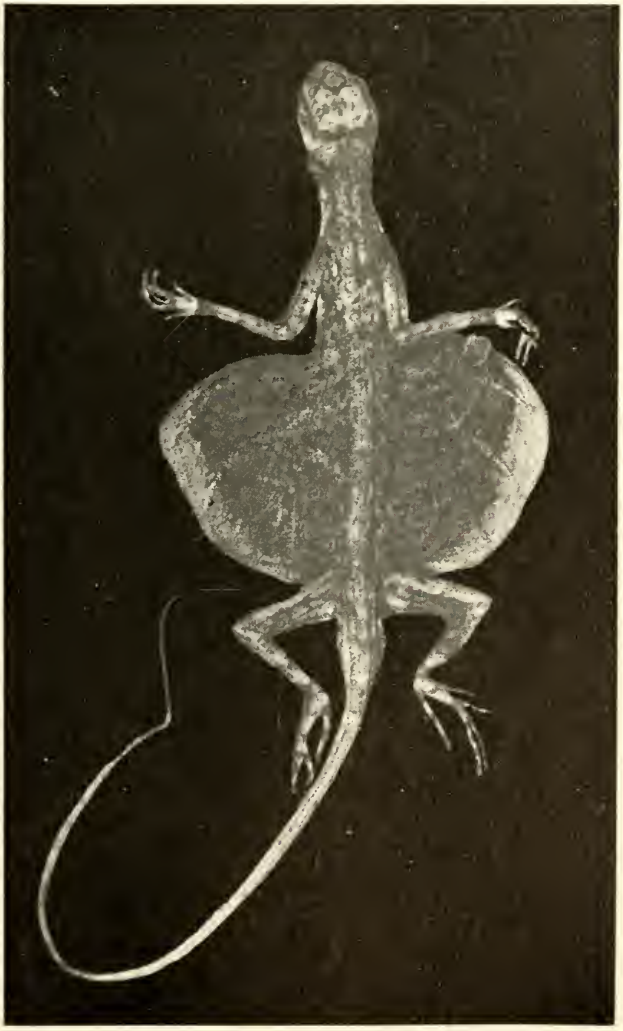


FIG. 43.—*Draco taeniopterus taeniopterus* Günther. No. 35864. Forest Experiment Station, Trang province, Thailand.

behind occiput; some black punctate spots on neck; body bronzy or grayish olive with a brownish W-shaped shoulder mark and two similar indefinite marks on back; wing-membranes olive-yellow with broken tranverse black bands about as wide as interspaces, some of which tend to bifurcate near the body; outer posterior part of wing maroon to magenta; underside of wing yellowish, transverse marks showing through membrane; basal part of dewlap and underside of wattles orange-red to carmine; distal part of dewlap pale green or olive; venter and underside of limbs yellowish; limbs banded with dark olive.

Measurements in mm. of *Draco t. taeniopterus*

NUMBER*	457	462	460	461	399
Sex	♂	♂	♂	♂	♀
Snout to vent	75	74	71	66	77
Tail	152	125+	140	136	153
Snout to arm	26	26	24.3	23	26
Axilla to groin	41	39	37	35	43
Wingspread	64	68	58	61	64
Length of dewlap	21	20	19	19	1
Head width	10	10	9.8	8	11
Head length	14.6	15.2	14	13	16
Arm	34	33	33	31	36
Leg	42	43	42	37	38

* Na Bon, Nakhon Si Thammarat.

Variation: The enlarged scales on the snout occasionally are arranged in an inverted Y-shaped series, but are more frequently as described in this specimen, in the material available to me. There is but little variation in color pattern. The color of the back does vary and in life may change in a few minutes from one shade of green or olive to another.

The large specimen mentioned by Malcolm Smith (1935, p. 140) "100 mm. from snout to vent, tail, 180" belongs to another species. (See M. Smith, Bulletin Raffles Mus., no. 13, Aug. 1937, pp. 75-76, where the statement is corrected.)

Distribution: The species ranges in Thailand from near the Malayan border to the province of Chiang Mai in the northwestern part of the country; it occurs also in southeastern Thailand. Presumably it has not been taken in the eastern or northeastern parts.

Outside of Thailand the species occurs in southern Burma and the Mergui Archipelago, and doubtless extends into Cambodia.

Remarks: The female lays four eggs. These have a small shelf-like projection at each end, similar to those on the eggs of *D. blanfordii.*

Draco blanfordii Boulenger

FIG. 44

Draco major Blanford (*nec* Laurenti), Journ. Asiat. Soc. Bengal, 1878, vol. 47, 2, p. 125; *ibid.*, vol. 48, 1879, p. 128 (type locality, Forest east of Tavoy, Tenasserim, Burma).

Draco blanfordii Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 267, pl. 20 (new name for *Draco major* preoccupied); The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 112; Fasciculi Malayenses, Zool. vol. 1, 1903, p. 153; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 61; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 3, 1915, p. 153; *ibid.*, vol. 2, no. 1, 1916, p. 53; *ibid.*, no. 2, 1916, p. 153; Bull. Raffles Mus., no. 3, 1930, p. 22; The fauna of British India, Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 141-142 (northwestern Thailand, Chiang Rai, southern Burma, Malaya); *ibid.*, no. 13, 1937, pp. 75, 76, pl. 8; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1091-1093.

Diagnosis: Large species, snout-to-vent length to 134 mm.; tympanum naked; nostrils directed upwards and outwards; head shields unequal, with or without an inverted Y-shaped series on snout; six scalerows between nasals; wing-membranes marbled with olive, usually with some five indistinct darker lines; a few brick-red flecks on upper membranes, posteriorly immaculate, yellowish below; red to salmon under wattles; gular appendage elongated, whitish, distinctly longer than head, with large transparent scales; throat nearly black; chin gray; median caudal scalerow elevated to form a low crest; a row of enlarged elevated keeled scales or groups of scales at base of wing-membranes.

Description of species (from No. 33680, Doi Suthep, Chiang Mai): Large species; rostral three-and-a-half times as wide as high, bordered behind by seven small scales, separated from nasals by one (or two) scales; nasals craterlike directed outward and somewhat upward, the length of one nasal about equal to distance between them; two median enlarged scales just back of level of nostrils, but no distinct inverted Y-shaped series discernible; canthal scales irregular but a series of elevated scales precedes canthus and continues above nasals; a slight constriction immediately posterior to nasals; supraorbital areas elevated; anterior supraciliary border with sharp-edged elongate scales; middle and posterior parts with small granular scales and with a rounded tubercle at posterior point; some enlarged scales on each side of occiput and one much enlarged keeled scale back of middle of eye, its posterior end reaching anterior level of tympanum; a few tubercular scales above and some-

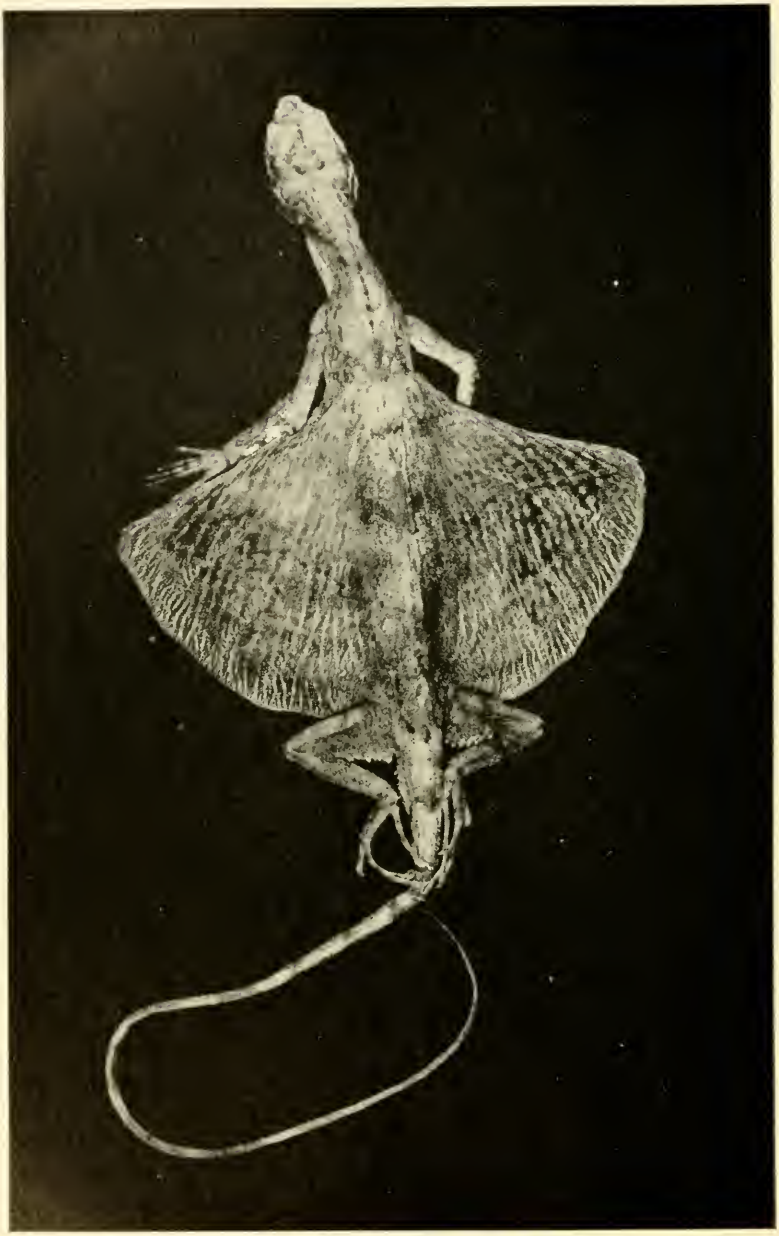


FIG. 44.—*Draco blanfordii* Boulenger. No. 469. Khao Chong Forest Experiment Station, Trang province. Actual snout-vent length, 102 mm.; total length, 280 mm.

what behind tympanum, one preceding it and one or two on cheek below it; nuchal wattles with several scales on upper surface distinctly larger than enlarged scales covering distal four fifths of the gular appendage; scales on dorsal part of body, small, somewhat unequal, distinctly smaller than ventrals, smooth or with a few scattered usually larger keeled scales; a spaced row of enlarged keeled elevated scales beginning on shoulder follow sides of the body to groin along base of wing-membrane; a very indistinct nuchal crest (in male); arm long, wrist reaching tip of snout; hind leg reaching or almost reaching axilla; fore- and upper-arm with enlarged keeled scales on upper surface; front of thigh and upper surface of tibia with enlarged keeled scales; one or two enlarged scales on posterior part of thigh; a fringe of enlarged free scales on back edge of thigh and on sides of base of tail; median scalerow on tail elevated to form a low crest for a fourth of its length.

Color: Above, on body, variegated grayish or grayish olive, mottled with lighter and darker; some indistinct blackish spots on neck and occiput; wing-membranes olive-gray mottled with darker olive and with some indefinite hair-fine darker lines; a few reddish or maroon flecks on outer posterior part of wing; under surface yellowish without black marks; venter as well as underside of leg and subcaudal region whitish; chin gray, growing nearly black on throat and around base of gular appendage; latter white, translucent; neck wattles red below; dark on front of shoulders. Tail banded with brown and gray; labials a little lighter than side of head.

Variation: The markings on the wings vary. Often the wings are practically unicolor, light or yellowish green with numerous longi-

Measurements of *Draco blanfordii*

NUMBER*	465	466	35704	194
Sex	♂	♂	♂	♀
Snout to vent	128	134	132	102
Tail	233	254	256	202
Head width	16	16	16	14
Head length	24	23	24	21
Snout to arm insertion	44	43.5	42.5	34
Axilla to groin	68	79	72	58
Greatest wingspread	125	124	122	114
Length of dewlap	37	31	36	8
Arm	52	51	53	44
Leg	58	60	64	56

* Na Bon, Nakhon Si Thammarat.

tudinal fine light lines formed of minute frosty flecks; other specimens may have a more or less distinct series of darker transverse bands across the wing, which may include a series of lighter areas. Several specimens have small blue-white spots covering the enlarged scales at the base of the wings and one specimen has a yellowish wash on the upper surface of the wing. Females lack the caudal crest, and have only a small dewlap.

My series consists of 13 specimens all but one of which is a male. The female has the typical coloration of "*cyanolaemus*" described from a female. Superficially in marking it resembles the pattern of *taeniopterus*.

Distribution: The species occurs in both northern and southern parts of eastern Thailand, specimens having been taken in Chiang Rai, Chiang Mai, Kanchanaburi, Phrae, Nakhon Si Thammarat, Phuket, Trang, Pattani, and Yala.

It is also known from Northern Malaya, and Burma as far north as the Dwana Hills. It has not been reported in the Indo-Australian Archipelago.

Remarks: Four eggs taken from the oviducts of the large female are oval, with the end "pinched" leaving a very narrow straight shelf on each end usually more pronounced on one end than other. The eggs measure approximately 14 x 7 mm. Whether eggs of most other species have this peculiarity I do not know. Once four eggs were dug up from the earth having this form but they could not be positively identified.

Draco formosus Boulenger

This form has three presumed subspecies, only the typical one occurring in Thailand.

Draco formosus formosus Boulenger

FIG. 45

Draco formosus Boulenger, Ann. & Mag. Nat. Hist., ser. 7, vol. 6, 1900, p. 190 (type-locality, Larut Hills, Perak, between 1500 and 3000 ft. altitude); Fasciculi Malayenses. Zoology, vol. 1, 1903, p. 152 (*part.*); Journ. Federated Malay States Mus., vol. 3, 1908, p. 65; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore, including the adjacent islands; Reptilia and Batrachia, 1912, pp. 61-62; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, pp. 153-154 ("Tanjong Mas and Bangnara," Pattani; Khao Wang Hip, Nakhon Si Thammarat; Maprit, Patiyu); *ibid.*, vol. 2, June 1916, p. 53 (peninsular and western Siam as far north as Lat. 14°30'); Journ. Federated Malay States Museum, vol. 10, 1922, p. 268 (Kuala Teku, Pahang, Malaya); Bull. Raffles Mus., Singapore, no. 13, Aug. 1937, pp. 75-76, fig. 2, pl. 8 (states that the female cotype is a specimen of *Draco blandfordi*).

Draco formosus formosus: Hennig, Temminckia, vol. 1, 1936, pp. 216-217, map no. 14.

Diagnosis: A large species (100 mm. snout to vent). Nostrils directed vertically upward; arm reaching somewhat beyond snout-tip; gular appendage of male with large blackish but translucent scales, not or slightly longer than head; tympanum naked. Wing-membrane with five more or less distinct cross-bands, outer part

FIG. 45.—*Draco formosus formosus* Boulenger. No. 35742, Khao Chong Forest Experiment Station, Trang province, Thailand. Actual length, 279 mm.

maroon; throat of both male and female and underside of lateral nuchal lappets, maroon or crimson (never green in female).

Description of species (from Bukit Besar, near Na Pradoo, Pattani, No. 34430): Rostral quadrangular nearly four times as wide as high, bordered laterally by two labials and eight small postrostrals; nasals large, craterlike, separated from rostral by one scale, from each other by five or six scalerows; nostril directed vertically upward; head scales unequal; a median longitudinal row of four keeled scales beginning between nasals terminates in middle of forehead; canthal scales enlarged, separated from nasals by three small scales; one enlarged keeled scale lies on snout touching canthals, the keel directed outward and backward; one or two enlarged supraocular scales on anterior edge of orbit; supraorbital areas elevated, the inner scales somewhat enlarged; a low rounded tuberculate scale at back corner of orbit; a very indistinct nuchal crest in male, absent in female; tympanum naked; an enlarged scale about midway between tympanum and nuchal crest; 10-9 supralabials each with a weak irregular keel evident near upper border and an indistinct keel on lower edge; above labials a slight shelf continued back under eye; ten infralabials with an upper and a lower ridge or keel on each; mental wider than long; scales subequal, smooth on body, with small groups of enlarged keeled scales along base of wings; ventral scales larger than dorsals, strongly keeled, keels directed inwards and backwards; gular appendage of male slightly longer than head, distal portion widened and covered with large quadrangular scales, somewhat translucent; small wattles on side of neck with large scales on outer upper surface; medium scalerow on tail forming a slight crest.

Arm extending length of second finger beyond tip of snout; leg reaches half way between axilla and elbow. A fringe of enlarged scales on edge of tail base and along back edge of thigh; scales on front of thigh and tibia enlarged.

Color in life: Above gray-olive with bluish and greenish flecks and occasional cream-colored scales; a black interorbital spot; two black spots on occiput and two on neck; back with a few indefinite dark markings continuous with dim darker lines crossing wings transversely; arms indefinitely banded; legs with some indefinite darker areas; toes banded in brown and gray; wing-membranes generally olive-gray above, the distal part maroon; under chin a dim gray reticulation; wattles dull pinkish above, while a large spot of

maroon covers underside of wattles and posterior part of gular appendage; most of gular appendage smoky-gray, the edges of enlarged scales whitish; breast, underside of limbs, venter, underside of thighs, and base of tail, white. Underside of wings grayish with an indefinite yellowish wash; distal part maroon as on dorsal surface; tail with broad bands of brown and gray.

Measurements in mm. of *Draco formosus formosus*

NUMBER	34430	35742	34851
Sex	♂	♂	♀
Snout to vent	99	101	89
Tail	146	170	163
Head width	12.5	13.2	12
Head length	19	19	17
Gular appendage	22	25	9
Arm	42	42	38
Leg	52	49	42
Greatest width of wing	42	42	37

No. 34430, Na Pradoo, Pattani; 35742, Khao Chong Trang; 34851, Bhetong, Yala.

Variation: The female specimen shows no trace of the nuchal crest but the color is practically identical with that of the male. Malcolm Smith (1937) has pointed out, that the female cotype of *D. formosus* is actually a *Draco blanfordii*.

The dark transverse irregular bands on the wings vary. In a female there are five, all enclosing lighter spots. The first (anteriormost) is very short, the second and third widest, the fourth longest, the fifth consisting of a few black flecks or small spots. The bars on the arms are very strongly defined, each bar having a lighter median part; those on the legs are similar but more indefinite.

The head-markings of the female include the interorbital spot, two small occipital spots (close together) and a pair of tiny spots on the neck; there are two dim transverse light bands across the head behind and in front of the black interorbital spot.

The scales in the fringe on the back of the thigh are largely cream in color. The tiny gular appendage is cream-white flanked on each side by pinkish or light maroon; underside of lateral nuchal wattles at least partly pink; yellowish brown (variegated) above.

Remarks: Specimens were found on forest trees usually at considerable distances from the ground.

Distribution: The species occurs in southern Thailand. It has been reported from Trang, Narathiwat,* Nakhon Si Thammarat and Chumphon.

It is known also in Malaya where it reaches from sea-level to 3500 feet altitude. Specimens formerly reported from Borneo and Sumatra are now regarded as belonging to *D. f. obscurus.*

Genus ACANTHOSAURA Gray

Acanthosaura Gray, in Griffith's Cuvier's Animal Kingdom, vol. 19, 1831, Suppl., p. 5 (type of genus, *armata.*)

Goniocephalus M. Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 157 (*part.*)

Diagnosis: Body somewhat compressed, usually with a rather sharp dorsal ridge and a dorsal crest larger in males; dorsal scales unequal, heterogeneous; a gular pouch may be present; a fold across shoulder usually conspicuous. Tympanum naked or partially covered by scales; tail somewhat flattened, the scales keeled and larger than dorsal body scales, longer than broad. No femoral or preanal pores.

In 1916 Malcolm Smith recognized four species in Thailand—*Acanthosaura armata* (with which was united *A. crucigera* Boulenger), *A. horrescens* Gyldenstolpe, *A. capra* Günther and *A. coronata* Günther.

In 1943 his opinions having changed, he united the genus *Acanthosaurus* with *Goniocephalus* and recognized three forms—*G. armatus crucigerus, G. armatus armatus* and *G. lepidogaster.* I am uncertain what specimen he has identified as *capra* for in this later work he mentions only four specimens of this species, none from Thailand. *Coronata* has been identified with Cuvier's *lepidogaster* after his having examined the types of Cuvier's species in Paris.

Three forms are known to occur in Thailand, a fourth should be searched for in the mountains of central northern Thailand. All known Thai forms have a postsupraciliary—and a lateral nuchal spine.

KEY TO SPECIES OF ACANTHOSAURA IN THAILAND

1. No diamond-shaped black mark on neck and shoulders; no Y-shaped series of scales on snout; tympanum large, naked; dorsal and nuchal crests separated by a small diastema 2 to 3 mm. in length; tail base swollen in males; a small nuchal pouch ..... *armata*

   A diamond-shaped black mark on dorsum of neck 2

* M. Smith's localities "Tangong Mas and Bangnara" Pattani, are now actually in the province of Narathiwat.

2. Spines of nuchal and dorsal crests separated by a diastema of seven to eight millimeters, the intervening space covered with small equal scales similar to upper body scales; nuchal black spot with "arms" reaching down on side connecting with diagonal black spot on shoulder. Head slenderer than in *armata*. Spine at supraciliary border and nuchal spine often as long as the diameter of orbit, *crucigera*

Spines of the nuchal and dorsal crests very close together but there is actually a separation since the spines at end of nuchal and beginning of dorsal crest may be shorter; postorbital and nuchal spines not half as long as orbit; no gular pouch; nuchal spot not connecting with diagonal mark on shoulder; spine on head less than half diameter of orbit ..... *lepidogaster*

Acanthosaura lepidogaster (Cuvier)

FIG. 46

Calotes lepidogaster Cuvier, Règne Animal, 2nd Ed., vol. 2, 1829, p. 39 (type-locality, Cochin-China).

Lophyrus tropidogaster Duméril and Bibron, Erpétologie générale, vol. 4, 1837, p. 413 (emendation for *lepidogaster*).

Acanthosaura coronata Günther, Proc. Zool. Soc. London, 1861, p. 187 (type-locality, Cambodia); The Reptiles of British India, 1864, p. 149, pl. 14, fig. E.

Acanthosaura lamnidentata Boulenger, Catalogue of the Lizards in the British Museum, vol. 1, 1885, p. 302, pl. 22, fig. 3 (type-locality Pegu, Tenasserim); The fauna of British India . . . Reptilia and Batrachia 1890, p. 126.

Acanthosaura hainanensis Boulenger, Proc. Zool. Soc. London, 1899, p. 957, pl. 66, fig. 2 (type-locality, Five Finger Mountains, Hainan).

Acanthosaura braueri Vogt, Sitz. Gesells. Nat. Fr. Berlin, 1914, p. 97 (type-locality, "S. China").

Goniocephalus lepidogaster: M. Smith, The Fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 161-162 ("N. Siam").

Diagnosis: A compressed median dorsal ridge on back surmounted by a low serrate dorsal crest; small spine behind end of supraciliary edge and a small nuchal spine somewhat above tympanum. A row of three or four scales from above tympanum extending towards eye, anterior end of the series not lower than upper level of tympanum; a nuchal crest of compressed scales, broad at their bases, separated from low dorsal crest by a narrow diastema; outer part of tympanum with small scales but never covering entire surface; a Y-shaped series of enlarged scales, usually if not always present on snout.

Description of species (from No. 35901, Doi Suthep, Chiang Mai): Rostral three times as wide as high bordered by two labials and five postrostral scales; nasal large separated from rostral by

two scales; a row of enlarged keeled scales on snout with two posterior branches forming an inverted Y-shaped figure; dorsal head scales unequal most of which are keeled, some rugose; canthal and supraciliary edge sharp, projecting outwards; a short spine behind supraciliary edge much less than half diameter of orbit;

FIG. 46.—*Acanthosaura lepidogaster* Cuvier. No. 1639 Doi Suthep, about 960 m. Chiang Mai province. Actual total length, 176 mm.

tympanum partly scaled over; row of three or four keeled scales from above tympanum to orbit, last much lower than upper level of tympanum; on back edge of occiput a transverse group of spines, one larger than others, directed upwards and backwards; strong nuchal crest of six to eight lanceolate spines their bases overlapping, the first two and last smallest; crest bordered by one row of enlarged, keeled and somewhat mucronate, erect scales; eleven or twelve supralabials, and a similar number of infralabials; mental small, separating first pair of postmentals which begin series of ten or twelve enlarged keeled scales; scales of chin angular, keeled, directed mesially, smaller than strongly keeled ventral scales; upper part of body with a compressed ridge, surmounted by a low dentate dorsal crest, separated from nuchal crest, terminating at base of tail; dorsal and lateral scales very small, intermixed with large keeled scales single or in small groups, sometimes in indefinite lines; scales point backward and upwards; small scales not smooth, some more or less keeled. Tail compressed, a half longer than head and body, all scales keeled strongly, the median subcaudal rows enlarged; a small diagonal skinfold from shoulder to near middle of neck; a slight gular pouch. Scales on arm keeled, mostly enlarged; third and fourth fingers subequal, with 17 scales below each, the scales doubly keeled with small spines or mucrones; fourth toe much the longest with 22 scales on its underside, most with a single keel. Leg reaches eye.

Color in life: Above, head dark black-brown, becoming more olive in occipital region. Side of head and orbital region with a blackish spot continued around back of occiput to a large black median spot which widens on shoulders; this spot bordered below by a clay-white line not quite meeting its fellow on median dorsal line; side of neck, tympanic area, and back part of labial area greenish yellow. Throat lively rose, the anterior labial and loreal regions pinkish white; venter yellowish with a greenish tinge. Underside of limbs and subcaudal area whitish; dorsum and limbs grayish brown with paired lateral black spots becoming brownish and fused on tail, forming large brown spots that are separated by light-gray bands; distal dark bands surround the tail. A very distinct dark-edged cream-spot on elbow, one on back of thigh and one across tibia; the two latter are contiguous when limb is folded.

Variation: The Y-shaped series of scales on snout and frontal area is more or less distinct in all specimens examined. The sharp com-

Measurements in mm. of *Acanthosaura lepidogaster*

NUMBER	36901 ♂	35902 ♂	33966 ♀	69 ♀
Snout to vent	76	72	85	91
Tail	118	104	104*	110
Total	194	176	189	201
Snout to arm insertion	28	28	37	31
Axilla to groin	38	35	42.5	46
Head width	16.3	16.4	20.3	21.2
Head length	22.6	21	27	28.5
Arm	41	39	45	46
Leg	67	59	65	70

* Incomplete; (all specimens from Doi Suthep).

pressed dorsal ridge is strongly evident. In the males available to me there is not much difference in height in either the nuchal or the dorsal crests, or between the two sexes.

Distribution: Chiang Mai, northern Thailand.

Remarks: When these specimens were found during a rain, they usually were dull brownish black, practically no trace of pattern being discernible. After a night in captivity the specimens displayed a maximum of bright color, the males always more colorful than females.

Several of the females contain eggs. No. 33966 has eleven, measuring approximately 7.5 x 10 mm. The stomach contents of this specimen consists chiefly of the remains of hymenopterous larvae. Wings identified as those of termites were also discerned.

Acanthosaura armata (Gray)

FIG. 47

Agama armata Gray, Zool. Journ., vol. 3, 1827, p. 216 (type-locality, Singapore.)

Acanthosaura armata: Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 240; Griffith's, Cuvier's The Animal Kingdom, vol. 9; Syn. 1831, p. 5, 1864, p. 148 (*part.*); Günther, Reptiles of British India, 1864, p. 148; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 301, pl. 22, fig. 1 (side view of head and body); The fauna of British India, Ceylon and Burma; Reptilia and Batrachia, 1890, p. 125 (*part.*); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 154, (*part.*).

Lophyurus armatus: Duméril and Bibron, Erpétologie générale . . . vol. 4, 1837, pp. 413-416.

Gonyocephalus (*Acanthosaurus*) *armatus:* Fitzinger, Systema reptilium, 1843, p. 44.

Gonyocephalus armatus armatus: M. Smith, The fauna of British India, Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 158-160, fig. 49; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, p. 1095.

FIG. 47.—*Acanthosaura armata* Gray. No. 2640 ♂. Na Pradoo, Pattani, Thailand. Actual snout to vent length, 118 mm.; tail, 166 mm.

Diagnosis: A spine behind orbit and one on side of neck, these nearly or quite as long as orbit; gular pouch absent; base of tails in males strongly swollen; supraciliary edge broadly overhanging eye; no Y-shaped series of scales on snout and frontal area; tympanum large, naked, somewhat smaller than eye-opening; no diamond-shaped black area on neck and shoulders; high nuchal and dorsal crest separate (one or two mm.); scales on sides minute with small intermixed tubercular scales.

Description of species (from No. 2640 ♂ Na Pradoo, Pattani): Head triangular in lateral or dorsal profile; interorbital and frontal areas sloping almost straight down to snout-tip, directed forward. Rostral small, bordered by a labial on each side, and posteriorly by five scales; nasal scales large, craterlike, the nostril directed outward and slightly backwards, separated from rostral by two scalerows. Head above covered by numerous scales of irregular size and shape, largest ones above orbital areas with three somewhat enlarged ones on median part of snout, but no Y-shaped arrangement; most scales keeled, the keels directed forward; interocular scales smaller, keels low, directed outward; a slight transverse ridge across occiput; scales a trifle larger than adjoining scales; a row of twelve enlarged scales begins at nostril and borders canthus and supraciliary edge to back of orbit, strongly projecting, the scales exposing a broad undersurface; a second row of larger scales border these above; a row of infraocular scales runs back and upwards and continues back to above tympanum, the series consisting of 18 scales, posterior largest. Between seventh supralabial and sixth canthal about 15 scalerows; mental small, its labial border smaller than rostral, enclosed behind by a pair of chinshields which are the beginning of an enlarged series of 15-17 scales, separated from labials by two rows of small scales, most of them with strong keels; a slight gular pouch evident (old male). A pair of erect elongated spines at back edge of orbit, touching last supraciliary, but separated from it at base; spine surrounded by two or three circular rows of pointed scales directed upwards; scales on back of occiput rather uniform but with small erect keels or spines. A pair of erect spines directed somewhat outward above tympanum on sides of neck, surrounded by a row of four elongate erect scales and a circular lower series of about twelve scales; nuchal crest begins a little in advance of these spines terminating in front of shoulders, consisting of ten compressed spines, first two shortest, and flanking these a similar number of erect scales alternating but

shorter, and one or two other similar rows of shorter scales. Dorsal crest similarly developed but near middle of back it reduces to a very low crest and continues as a row of keeled submucronate scales to tail; scales on sides of neck and body small, erect, subimbricate, keeled, or spinelike, points directed upwards in upper part of body, gradually directed backwards lower on sides; scattered enlarged keeled scales on sides and back, the small scales being 20-22 per centimeter; scales on chin larger than body scales, keels directed backward; scales on venter much larger than dorsals (eight to a centimeter) very strongly keeled, the keels directed backwards and on sides of venter slightly outwards; in preanal area about ten transverse scalerows three of which are larger than others; base of tail much swollen; subcaudal scales enlarged, elongate, sharply keeled and mucronate; scales on front surface of upper and lower arm rather large; leg similarly scaled; eye opening diagonal (8 mm.); tympanum naked, its greatest diameter 5 mm.; length of forward directed postorbital spine, 7.2 mm.; hemipenes extruded, each showing two primary lobes one centimeter long, strongly honeycombed with rather deep pits, and each lobe again divided distally into two short lobes; arm pressed forward, wrist reaches tip of snout; leg adpressed, fourth toe reaches halfway between tympanum and eye.

Color: This specimen is nearly uniform brownish fawn the head a little more brownish with only very indefinite traces of a dorsal reticulation; a dim diagonal black line in front of shoulder overhung by a diagonal skinfold. Tail gray-brown with narrow light bands above; chin and throat with very dim longitudinal darker lines; venter and much of subcaudal region white; limbs grayish brown, banded dimly.

Measurements in mm. (of Nos. 2640 ♂ and 2641 ♀): Snout to vent, 118, 108; tail, 166, 139; snout to arm-insertion, 43, 35; axilla to groin, 58, 54; height of head, 24, 22; length of head, 33, 30; width of head, 23.5, 21.5; arm, 68, 58; leg, 88, 80.

Variation: A female specimen, No. 2641, from the same locality (Na Pradoo, Pattani), has a reticulate gray-brown pattern enclosing somewhat elongate lighter fawn areas; the chin and throat has a median whitish stripe bordered by two longitudinal black stripes with two or three other parallel dark lines less distinct; head darker brown with some dark lines radiating from about eye; a dark diagonal line in front of shoulder partly hidden by a skinfold in the area; venter and under limb whitish, two light spots on pos-

terior upper surface of leg; digits with bars of brown and fawn. The crests are lower.

Distribution: This form described from Singapore is found throughout Malaya and probably reaches no further north than the Nakhon Si Thammarat Mountains in the province of that name. It has been reported in Sumatra, Tenasserim and Cochin China. I cannot vouch for these three reports.

Remarks: This species was found on Bukit Besar at or near Na Pradoo. It occurs with another species which is here identified as *crucigera.* Since the two forms exist together and each maintains its own structural characteristics they cannot be regarded as members of the same species. The second form has the scales more imbricating, the ventral scales large (7 to a centimeter) head strongly banded, venter brown spotted, throat and chin black, and much lower spines and crests. In the form described the minute hairlike spines on each scale are conspicuous under a lens.

Acanthosaura crucigera Boulenger

FIG. 48

Acanthosaura armata (part.) Blanford, Journ. Asiat. Soc. Bengal, vol. 48, 1879, p. 130.

Acanthosaura crucigera Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 302 (type-locality Tavoy, Burma); The fauna of British India, Ceylon and Burma; Reptilia and Batrachia, 1890, p. 125; A vertebrate fauna of the Malay peninsula . . . Reptilia and Batrachia, 1912, p. 69; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, p. 154, 1915 (*part.*); *ibid.*, vol. 2, June 1916, p. 53 (*part.*); (unites *crucigera* and *armata*); The fauna of British India, Ceylon, and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 160-161 ("Peninsular Siam, Patani, Isthmus of Kra, Tenasserim and the adjacent hills of Siam; hills north of Pre and Dong Paya Fai Mountains in N. Siam; S. E. Siam (Chantabun [= Chanthaburi]); [island of] Koh Chang and the adjacent territory in Cambodia."

Diagnosis: Spines of nuchal and dorsal crests usually broader at base than in *armata,* and the two crests separated by a greater distance (seven to eight mm.), the intervening space covered with small equal scales, similar to those on sides of neck; a black nuchal spot, narrowed much on either end, and connecting with the black diagonal band on front of shoulder, roughly cruciform in shape although considerably widened on shoulders; body and head slenderer than in *armata;* scales under tail forming transverse rows curving forward somewhat, the scales longer than wide; tympanum naked, distinctly smaller than eye-opening; a spine present at back edge of orbit, and one on side of neck their height much less in each case than half diameter of orbit; crests low, especially dorsal, situated on a sharp median elevated ridge; crest scales widening on

base of tail, and terminating behind level of vent. Leg, pressed forward, reaches near to nostril; no Y-shaped series of scales on snout and frontal area.

Description of species (from No. 192 Na Bon, Nakhon Si Thammarat): Body compressed forming a relatively high median ridge, surmounted by a dorsal crest; body triangular in cross-section. Head

FIG. 48.—*Acanthosaura crucigera* (Boulenger). No. 192, Na Bon (hydroelectric dam) Nakhon Si Thammarat, Thailand. Actual length, snout-vent, 103 mm.; tail, 146 mm.

generally triangular seen in lateral profile; rostral wider than high, bordered laterally by a labial and posteriorly by five scales; scales on snout larger than those in *armatus* (12 between fifth canthals; 16 or 17 in *armatus*); eight scales between nasals (12 in *armatus*); median row on snout a little larger and more strongly keeled than other; scales on snout smooth or with keels, the keels variously directed; some scales near tip of snout equally as large or larger than scales in supraorbital region, most of which are keeled, the keels directed forward; nasals large, craterlike, separated from rostral by one scale; nostrils directed outward; a series of 13 canthal-supraciliary scales overlapping somewhat and overhanging eye the edge not serrate; an elongate erect conical spine at back edge of orbit, surrounded by six pointed scales and an outer circular row of about ten erect smaller scales; a low transverse occipital ridge behind which scales are unequal, rather large, and conical; an erect spine on each side of neck surrounded by four erect keeled compressed scales; a suborbital scale series not continuous with enlarged scale series running from orbit diagonally backwards and terminating above tympanum, consisting of six thickened keeled scales; tympanum naked; supralabials, 12-12, row bordering supralabial above not enlarged; 11 scales between fifth labial and fifth canthal; infralabials, 11-11; mental about one third as large as rostral, bordered behind by two scales, each the first of series of seven enlarged sublabials, separated from infralabials by one row of scales posteriorly; scales on chin and throat somewhat erect, keeled, and usually mucronate.

Nuchal crest consisting of seven erect spiny scales flanked laterally by three rows of smaller erect scales; an interval of seven millimeters between this crest and dorsal crest; latter consisting of low scales strongly compressed, widened at base, the erect tips pointing upward and somewhat backwards; on rump these scales become somewhat flatter and wider, the series continuing for a short distance on tail; this crest flanked by one or two compressed erect rows of scales much lower than those of crest. Scales on sides of neck and body imbricate, subequal, angular, the angles pointing upwards and backwards, with large flat scattered keeled scales intercalated. Scales lower on sides and on posterior part of sides point nearly directly backwards. Tail of female not widened, rather triangular in cross-section at base; subcaudal scales forming curving transverse rows, scales longer than wide; four short rows of enlarged scales in preanal region; ventral scales large, strongly keeled, in regular longitudinal and diagonal rows, the keels forming lines directed

somewhat outwards; scales larger than in *armatus* (six in a centimeter); scales on upper surface of arm with enlarged keeled scales; scales on femora large, rather regular in front; on upper and posterior sides scales irregular, some much enlarged; scales large, more regular, on tibia; 22 keeled thickened lamellae under fourth toe; third and fourth fingers equal; a skin-fold in front of shoulder. Tympanum moderate (4.8 mm.); length of eye-opening, 5.5 mm.; height of postorbital spine, 5 mm.; height of highest nuchal spine, 4.8 mm.; highest spine in dorsal crest, 2.8 mm.; arm brought forward the wrist reaches one-half centimeter beyond snout; leg adpressed, the toe reaches middle of eye. Each ovary with five eggs.

Color in life: Front of head with transverse bars of black and green, the most prominent green one crossing orbital region; third black bar forms a median angle; lips yellow with a series of black spots, parts of radiating lines from eye; eye black; body with a deep black reticulum enclosing yellowish to brownish yellow spots; spots larger posteriorly; a whitish or whitish-yellow ocellated spot at knee and elbow, with certain others indicated on arm and leg; venter creamy with some metallic green reflections and with black spots or vermiculations; an elongate black nuchal spot widening on shoulder and fusing with a dark diagonal line in front of shoulder; chin and throat blackish with a suggestion of a nuchal pouch; arms with darker and lighter marks above; legs darker above with suggestions of brown bars below. Tail banded with dark-brown and dirty light-brown.

Measurements in mm. (Nos. 192 ♀, 3887 ♂, and 3885 ♀): Snout to vent, 103, 95, 97; tail, 146, 81 *, 135; snout to arm-insertion, 35, 38, 32; axilla to groin, 52, 49, 46; length of head, 29, 25, 25; width of head, 20.8, 18, 19.5; height of head, 16, 15, 15.2; arm, 54, 56, 54; leg, 83, 88, 75.

Variation: The two specimens (Nos. 3885 ♀, 3887 ♂) from Na Pradoo, Pattani, were taken at "rather low elevations" on Bukit Besar. The body of the female contains ten large eggs (one centimeter in diameter). The width of the distended body is 35 mm. The area on the side of neck below the nuchal spot is cream, the color extending onto labials. The lateral reticulum is less distinct and there is a series of somewhat indefinite large brownish spots on the upper part of body. The spotting on venter is reduced. The male (No. 3887) strongly resembles the male from Na Bon, Nakhon Si Thammarat, some 200 km. north.

* Incomplete.

One young specimen from Na Pradoo, No. 3886, resembles the female No. 3885. The venter has a distinct reticulum. There is a dark line on the supralabials and one bordering the infralabials.

Distribution: In Thailand the species occurs in the peninsular provinces. Outside of Thailand it occurs in Burma, the type-locality being Tavoy.

Remarks: The intestines especially the colon of three specimens examined, were packed with feces containing very few identifiable insect remains, but seemingly much earth and sandgrains. One suspects that this may be engulfed with earthworms. The species is terrestrial.

Genus GONIOCEPHALUS Kaup

Gonocephalus Kaup, Isis, 1825, p. 590 (corrected to *Goniocephalus*), 1827, pp. 610-614 (type *tigrinus* = *chamaeleontinus*).

Gonyocephalus: Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 282.

Diagnosis: Body strongly compressed; a gular pouch usually evident at least in males; dorsal scales unequal in size and shape; a dorsal crest; tympanum naked, superficial. A fold in front of shoulder extending onto throat; tail compressed; no preanal or femoral pores.

Three species are present in the fauna of Thailand. All confined to the southern part of the country. These are *Goniocephalus grandis, G. abbotti,* and *G. borneensis.* Although, in a previous paper (Taylor and Elbel, 1958) I followed Malcolm Smith in regarding *Acanthosaura* a synonym of *Goniocephalus,* more careful study of the forms, especially in the field, leads me to believe that this is not the true relationship. In this work I am regarding *Acanthosaura* a separate genus.

KEY TO THE SPECIES OF GONIOCEPHALUS IN THAILAND

1. Supraciliary border strongly elevated; dorsal crest almost as high as nuchal crest; a row of five enlarged scales on the sides ..... *abbotti*
   Supraciliary border not strongly elevated 2
2. Enlarged scales scattered over sides; nuchal and dorsal crests continuous, very high in the male; dorsal, gular, and ventral scales strongly keeled ..... *borneensis*
   No enlarged scales on sides; nuchal crest very high in males, composed of long spines united together and free only at tips; a notch between nuchal and dorsal crests; gular and ventral scales smooth, *grandis*

These animals are usually to be found in high trees. The young of *grandis* may be terrestial and somewhat aquatic. A group of

young that I believed to be the young of *grandis* were seen on the tip of a small peninsula at Songkhla in shrubs growing in a pool. When disturbed these lizards would take to the water and swim under water to another clump of shrubs also in the same pool. None were captured since they were discovered when I was on the point of leaving the city. If they were not the young of *grandis* they were certainly no known species occurring in Thailand.

Malcolm Smith has placed *Goniocephalus abbotti* as a synonym of the Bornean form *G. doriae*. The differences that obtain would seem to preclude this association.

Goniocephalus abbotti Cochran

Gonocephalus abbotti Cochran, Proc. U. S. Nat. Mus., vol. 60, 1922, pp. 1-3 (type-locality, Trang, Thailand).

Gonocephalus doriae: M. Smith, Bull. Raffles Mus., no. 3, 1930, pp. 24-25 *part.* ("Benang Star," Yala, Thailand).

Diagnosis: Large species with canthus rostralis strongly projecting, and supraciliary border strongly raised, forming a sharp posterior angle; a series of much-enlarged dorsolateral scales. Nuchal and dorsal crests continuous, the crest distinguishable far onto tail. Body and tail strongly compressed; tail with eight dark bands separated by lighter bands of pinkish fawn.

Description of species (from No. K58, Boonsong Lekagul collection, Yala, Thailand): Body and tail very strongly compressed; head triangular, frontal area directed almost straight forward; rostral small, about as wide as high, bordered on each side by a supralabial, behind by three scales, the median enlarged; tip of snout somewhat elevated; nostril in a somewhat elevated nasal that is separated from rostral by three (or two) scales; canthus rostralis sharply defined, projecting, elevated, continuous with sharp supraciliary border which is strongly elevated reaching back to level of eye, then forming a sharp angle; snout, frontal and supraorbital areas, covered with small smooth unequal scales, largest being a series of three median scales on snout; peripheral scales large folded over edge with an upper and lower face exposed; a strong depression in occipital region with a few larger scales; loreal region nearly vertical, scales two or three times larger than those in orbital area. Eleven supralabials, followed, to angle of mouth, by several tiny scales; twelve to thirteen infralabials, followed by a few tiny scales to mouth-angle; diameter of orbit (16 mm.) only slightly longer than snout (15.6 mm.); tympanum distinct, its greatest diameter (6 mm.) less than length of eye-

opening (8 mm.); no enlarged scales above tympanum; a few just posterior to middle of orbit; mental very small, touching two enlarged scales the first of two series of scales, anterior ones larger than labials; a small distinct gular pouch and a transverse nuchal fold; a row of small median serrate scales begins near tip of chin, and runs back to base of gular pouch. Nuchal crest high, but less than diameter of orbit, continuous with dorsal crest which continues far onto tail; crest-scales triangular, serrate, anterior ones pointing slightly backwards; at base of crest-scales a row of equally large scales pointing upwards; below these on sides two other rows somewhat larger than lateral scales; lateral scales subequal, except a row of five enlarged scales beginning on shoulder and extending to above groin; low on sides scales increase in size to equal the smooth scales on venter, which are two to four times larger than lateral scales; most scales on chin and gular pouch small; caudal scales considerably enlarged, there being seven or eight rows at base; two subcaudal rows strongly keeled to near tip. Scales on outer faces of limbs larger than those on concealed surfaces; leg reaches eye; third and fourth fingers subequal in length; 23 scales under fourth toe; basal part of toes with two rows of scales, both keeled, keels terminating in spines, but toward end a single row, each scale with two keels; terminal scale much widened, equal to that at base of claw above. No preanal or femoral pores.

Color in preservative: Head greenish olive with several radiating dark lines above eye and two or three dim darker lines behind orbit; sides olive-tan with numerous longer or shorter black irregular striations on neck and sides; arms and legs brownish (when epidermis is shed the color is lavender), with some ivory marks on back part of forearm and front part of thigh; chin greenish yellow. Venter and underside of limbs ivory-white; tail with nine bands of brownish olive, the bands growing longer posteriorly and separated by subequal pinkish-fawn bands.

Measurements in mm.: Snout to vent, 140; tail regenerated for nearly half its present length; snout to angle of jaw, 45; snout to angle of supraciliary border, 34; greatest width between supraciliary borders, 25; greatest depth of body, 40; greatest depth of tail, 21.5; arm, 84; leg, 112.

Distribution: The type-specimen came from Trang, and three other specimens have been taken in the province of Yala.

I have seen a specimen from Gunong Tehu, Kuala Trengganu, Malaya.

Remarks: An examination of the Gunong Tehu specimen elicits the following data: The scales on the venter are large, smooth and the character of the scales on the limbs are practically identical in size and number of rows with the specimen here described. A slight fold of skin is evident back of the occiput, rising above tympanum and terminating on the midline near the occipital spot. In the described form it is not indicated. The height and character of the crests is the same in both; both have the row of enlarged distant scales begin near midway of the back somewhat below the base of the crest. The tip of the snout is elevated in both.

The species inhabits large forest trees and probably for this reason has remained rare in collections.

Goniocephalus borneensis (Schlegel)

Lophyurus bornensis, Schlegel, Bijdr. tot de Dierk., vol. 1, 1848, p. 6, pl. 3, fig. 2 (type-locality, Borneo?).

Gonyocephalus borneensis: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 288; *ibid.*, vol. 3, 1887, p. 493; Fasciculi Malayenses; Zoology, vol. 1, 1903, p. 153; Journ. Federated Malay States, vol. 3, 1908, p. 65; Robinson and Kloss, Journ. Federated Malay States, vol. 5, part 3, Oct. 1914, p. 154 ("Kao Nawng, Bandon *); Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 53 (Bandon); Boulenger, A vertebrate fauna of the Malay Peninsula; Reptilia and Batrachia, 1912; pp. 65-66.

Diagnosis: A large lizard reaching a snout-vent length of 138 mm. a tail length of 328 mm.; a supraciliary and canthal ridge continuous, not strongly raised; a gular sac well developed; usually a Y-shaped series of larger scales on snout; an enlarged tubercular scale on each side of occiput; nuchal and dorsal crests continuous, composed of separated lanceolate scales, most of them as long as or longer than diameter of orbit; a diagonal fold across shoulder, tending to meet its fellow on throat; tympanum distinct. Body and tail compressed.

Description of species (from EHT-HMS No. M. 2 (8623)): Head with the canthal and supraciliary edges continuous, somewhat overhanging, reaching summit above eye and descending a short distance behind eye; rostral moderately large, bordered laterally by a supralabial and seven postrostrals; nostrils in a single nasal, separated from the rostral by a single scale, and from its

* This locality (lower camp) is described as "situated on the upper reaches of the river flowing past Ban Kok Klap, probably about fifteen miles distant from that place at a height above sea-level of about 1,200 feet and quite close to the divide leading down to Nakon Sitamarat."

A second camp, Kao Nawng (upper camp) was established also. "During our stay on the mountain a part was detached for work at higher elevations and a camp was established at about 3,500 feet, a few hundred feet below the extreme summit of the range in a saddle between two peaks."

fellow by eleven scalerows; scales on top of head rough, irregularly keeled; a more or less distinct Y-shaped series of scales on snout; frontal and interorbital areas depressed, scales smaller than supraorbital scales; a pair of spinelike scales in occipital region; eleven supralabials, two or three showing faint keels near their lower borders; ten infralabials. Mental rather small bordered by two labials and two enlarged scales, each first of a series of three or four enlarged scales; a throat pouch (better developed in old males); scales on sides of body small, somewhat variable in size growing larger near crests and low on sides; scales pointing upward on upper anterior part of side; farther back and lower on sides they may be directed backwards or backwards and downwards; scales on chin and venter strongly keeled, those on chin and throat smaller; a diagonal skinfold in front of shoulder reaching throat followed by a small depressed "pocket" with fine scales; arms and legs with large keeled scales, keels often forming continuous lines; scales on compressed tail much larger than those on sides; several rows of heavily keeled scales under base of tail; a very small serrate crest indicated on base of tail; nuchal and dorsal crests continuous, the crests composed of narrow soft compressed lanceolate spines longer than diameter of orbit; on each side of crests two or three rows of small upright soft spines, outermost shortest; an indefinite dorsolateral row of enlarged scales with other enlarged, often tubercular, scales lower on sides; some enlarged scales above, below, in front, and behind tympanum which is well developed, superficial; a slight fold of skin just back of occipital region beginning above tympanum. Leg reaching nostril; twenty-three scales under fourth toe; basally there are two scales, each keeled distally.

Color: Top and sides of head olive; throat-pouch bluish, the scales with black bases; side variegated olive and lavender with some blackish flecking. Enlarged scales often blue; dorsal and nuchal crests bluish to ultramarine with black at base of crest above shoulders; tail banded gray-olive and whitish. A blackish area in front of shoulders; venter and under thighs amber.

Measurements in mm.: Snout to vent, 130 mm.; tail, 278 (tip missing); width of head, 25; length of head, 40; diameter of orbit, 13; length of snout, 16; height of nuchal-crest spines, 18; dorsal crest, 13; arm, 76; leg, 112.

Variation: The described specimen has the head scales larger and rougher than two other specimens examined. There is a decided swelling back of the angle of the mouth in older males. Most

of the scales of the body are keeled and often mucronate; a single hairlike projection extends from below the apex of the scale. A few of the head scales lack a spine and may have two or three small hairs. The sutures of the labials may be dark.

Distribution: The species, first discovered in Borneo, has been taken in Malacca, Perak (3600 ft.), Pahang, and Selangor.

In Thailand it has been reported only once near the border of Surat Thani and Nakhon Si Thammarat. Two camps are mentioned at Kao (Khao) Nawng, one at 1500 ft. one at 3500 ft. The report by Robinson and Kloss does not give the elevation.

It lives in high trees and is not easy to detect. It probably occurs in suitable mountain localities from Surat Thani south into Malaya.

Goniocephalus grandis (Gray)

FIG. 49

Dilophrys grandis Gray, Catalogue of the lizards in the collection of the British Museum, 1845, p. 239; Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 640, pl. 20; Günther, The reptiles of British India, 1864, p. 136.

Gonyocephalus grandis: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 298; The fauna of British India, Reptilia and Batrachia, 1890, p. 124; Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 153; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, p. 66; M. Smith, Bull. Raffles Mus., no. 3, 1930, p. 24 (Setun [Setul]).

Diagnosis: A large species with a snout-vent measurement often exceeding 155 mm. with a total length of 405 mm.; crests outlining top of head, especially supraciliary border, not very strongly elevated (compared with *abbotti* and *chamaleontinus*); nuchal crest not continuous with the dorsal crest but very strongly elevated, built up of several superimposed rows of scales surmounted by about 30 scales, middle ones greatly elongated, connected with each other but with a short free serrate edge; after an interval, a dorsal crest less than half elevation of nuchal crest, the individual elongate scales fused except for a serrate edge, terminating posteriorly on a level with vent. Body and tail compressed; snout somewhat depressed above.

Description of species (from No. M. 138,* EHT-HMS collection from Bukit Lagon Forest Reserve, Kepong, Selangor, Malaya): Rostral small, barely in contact with a labial on each side, and followed behind by five postrostrals; nostril pierced in a single nasal, that is separated from rostral, and likewise from supralabials by two or three scales; nasals separated from each other by about 12

* Males in the collection from Thailand are immature and I have chosen an adult Malayan male for the description (received through the courtesy of Mr. Lim Boo-Liat).

FIG. 49.—*Goniocephalus grandis* (Gray). No. 34678 ♀. 14 km. northeast Bhetong, Yala. Actual snout-vent length, 112 mm.

scales; canthal and supraciliary scales continuous, enlarged, separated by a gap from postocular series; anterior part of snout flattened but a slight longitudinal ridge present on middle of frontal area; supraorbital areas elevated, limited mesially by a curving row of larger scales; these rows separated by ten scalerows, occupying a deep depression between them; scales in middle of supraorbital areas somewhat larger than others. A strongly curving series of somewhat enlarged scales paralleling posterior curve of orbit with a short row of similar scales extending back from it to above tympanum, terminal scale largest; another enlarged tubercular scale between tympanum and crest; tympanum moderate, superficial, its greatest diameter (6 mm.) greater than half length of eye-opening (9.5 mm.); length of snout in front of eye (18 mm.), greater than diameter of orbit (15 mm.); twelve or thirteen supralabials, last small; eleven or twelve infralabials; mental small, triangular, bordered by a labial on each side, and two enlarged scales first of two series of four. No longitudinal serrate series of scales on chin and throat; nuchal pouch scarcely indicated; diagonal fold on neck is indicated; a distinct swelling on area behind jaw-angle; scales on middle of chin and neck smaller than those along infralabials and on swellings. Scales on sides of neck and body very small, subequal, smooth, becoming a little larger as they approach the venter and dorsal crest. Scales on venter subequal, larger than other scales on body; scales on tail about size of ventral scales, except that two median scalerows below tail are enlarged and keeled on basal half. Body and tail strongly compressed.

The nuchal crest consists of several fine series of scales surmounted by four larger series, one above other, pointing upwards and these surmounted by a weblike series of about 30 scales, small anteriorly and posteriorly but much elongated mesially with a short serrate edge; this extends from near level of orbits to above arm-insertion. Dorsal crest beginning shortly behind notch following nuchal crest, composed of elongate spines pointing upward, together forming a weblike structure with a short serrate edge above, terminating above vent.

Arms and legs strong; wrist reaching snout, leg reaching front of orbit; middle fingers equal in length; 36 lamellae under fourth toe, each with a median keel. Scales on sole and palm keeled or spinose; many scales on limbs and base of tail beset with three or fewer fine hairlike structures emerging from posterior part.

Color: Generally lavender-brown above with a series of bluish-gray bands on limbs and digits; venter lavender-olive with about

ten cream ventral bands reaching sides and continuing as a series of separate cream spots covering six to ten scales; these may reach halfway up on sides of body; tail strongly banded in bluish white and brown bands, narrow basally but growing longer distally; ten or eleven bands of each color. Chin and throat cream with olive-brown longitudinal streaks. Nuchal crest light brown, dorsal crest nearly lavender.

Measurements in mm. of *Goniocephalus grandis*

NUMBER	M. 138	34434	34678
Sex	♂	♀	♀
Snout to vent	154	100	112
Tail	396	194	145
Snout to arm insertion	60	38	46
Axilla to groin	70.2	45	49
Head width	36	20	18
Head length	51	30	32
Height of nuchal crest	26	6	6
Height of dorsal crest	13	2	2
Arm	78	53	57
Leg	127	85	98

Variation: Two young specimens from 15 km. NE of Bhetong, Yala, were brown in life, the nuchal crest variegated brown with a light-tan band from eye running back and meeting its fellow on the notch following the nuchal crest; below this, beginning on eye, a broad dark-brown band, involving upper part of tympanum, passes back joining its fellow on shoulder; four other diagonal bands cross body more distinct in the younger smaller specimen (No. 34434).

The larger specimen No. 34678 has the terminal 65 mm. of the tail regenerated. It is cylindrical rather than compressed and the scales are sharply keeled and often spinose rather than smooth. This is in odd contrast to the basal part of the tail. The ventral surface is an indefinite brownish white clouded but not showing clearly the ventral bands although these are indicated on sides. The streak under chin and throat are indicated.

A single female from Malaya was examined. This shows, the head dark brown above with five or six very narrow light transverse marks; two light chevrons on neck bordered by two black chevrons, the lower widening somewhat on shoulder; four or five other light chevron bands across back, each with a dim darker

median line separated by wide dark area on upper part of sides while lower sides are speckled with light spots; the ventral bands are obscured; arm, hand, tibia, and foot strongly banded with gray; chin streaked. The nuchal crest on the female is low but distinguishable, but the dorsal crest can scarcely be said to be present. Snout-to-vent length is 125 mm.

A large male (No. 182 Raffles Mus.) from Pulao Tioman shows the streaks under chin and throat blue with considerable bluish color low on the sides and less on venter. This specimen is generally darker (nearly blackish on sides. Its snout-to-vent length is 150 mm.).

Distribution: The species is known in the following Thai provinces: Setul, Yala, Songkhla, and Pattani.

Outside of Thailand the species occurs in Sumatra, Borneo, Nias, Mentawei Islands, Malaya, and Pulao Tioman.

Remarks: Specimens occasionally are seen in shrubs or small trees growing in small ponds or streams. These may dive and swim several meters underwater.

Genus Calotes Cuvier

Calotes Rafinesque, Anal. Nat., 1815, p. 75 (*nomen nudum*).

Calotes Cuvier, Règne Animal, vol. 2, 1817, p. 35 (type, *Lacerta calotes* Linnaeus).

Lophodeira Fitzinger, Systema reptilium, 1843, pp. 15, 46 (type *Bronchocoela cristatellus* Kaup).

Diagnosis: Teeth mostly acrodont, compressed except canines and incisors which are at least semithecodont and may be replaced; body compressed for arboreal habitat; tail often two to three times length of head and body; a dorsal crest usually present, higher in males; femoral and preanal pores absent.

The genus is distributed throughout southern and southeastern Asia from Afghanistan and the Thibetan border through India to Ceylon; east to southern China, Indo-China, Malaya; through the Malayan Archipelago to the Philippines but not reaching to New Guinea.

In Thailand the genus is represented by five well-defined species each showing considerable variation in the number of scales around the middle of the body and in color and markings. It seems probable that this scale variation betokens subspecific differentiation worthy of recognition in some populations; however, insufficient material is available to me, to make a decision on the matter.

Certain of these variables have already been named and thrown into synonymy by other workers.

The ability of these animals to change color is probably not exceeded even by the chamaeleons. A brilliantly colored male may in the matter of one or two minutes change so as to be unrecognizable as the same individual. The sexual differention is strongly marked. In males of the various species the gular pouch is more or less developed; the nuchal and dorsal crests are higher, and the coloration, at least during the breeding season, is much more brilliant than in females.

Courtship has been observed in several species. I quote from Malcolm Smith (1935, p. 198) on *Calotes mystaceus:* "The courtship which continued until the eggs were laid . . . consisted for the most part of absurd bowings and noddings of the head. This was commenced by the male, and usually, after a short time, responded to by the female. The pair faced each other on these occasions, arching their backs and puffing out their throats to the full extent. The vivid hues assumed by the male (and slightly so by the female) during this performance transformed him into a truly gorgeous creature. The head and fore-part of the body became of a light electric blue, sometimes green colour, the gular pouch dark purple, whilst the pale stripe which borders the upper lip and passes on to the shoulder turned almost white and stood out in strong contrast to the other colors."

Deposition of the eggs by the female is usually accomplished after the female has dug a hole in relatively hard earth. I have watched and reported on the egg-laying of a Ceylonese species, *Calotes calotes.*

Several specimens of this species, normally a dark green animal with vertical whitish spots, were discovered digging in the hard earth of a well-travelled elephant-path. All were now nearly black without scarcely a trace of the green color. The holes were of various depths. In none were eggs seen at this time.

Somewhat later in the day, I observed a single female depositing eggs in a completed hole. After a certain number of eggs were deposited, the loose dirt was dragged over them and, using the head as a pile driver, she pounded the earth above them. Then followed another period of egg laying and a similar filling in of the hole with loose earth, and the same pounding tactics. After the last egg had been laid the hole was completely filled in and pounded until the

surface was on a level with the surrounding earth. Then, fragments of leaves, sticks, and other objects were spread over the area hiding the location of the nest from possible predators.

Color changes in the lizards may be induced by various means. A specimen captured in the daytime and placed in a dark collecting bag may change to less colorful hues; on the other hand, specimens of a dull-colored male after a night in captivity may appear highly colored. The changes also take place during the sexual excitement of courtship. Smith reports that fear such as is induced by placing a serpent with captive specimens, will cause the male to assume his brilliant nuptial colors. "They invariably faced the snake bowing to it and nodding their heads exactly as when courting. The crest was strongly erected, the pouch fully distended, and the colours became gradually more vivid until they were almost as intense as during sexual excitement."

The Thai name is *ginka* and is widely used in areas where Thai is spoken, for the various species of the genus *Calotes*. In places the name is also applied to species of *Goniocephalus* and *Physignathus*. Species of the gliding ("flying") lizards are members of the same family *ginka-bia*.

KEY TO SPECIES OF CALOTES IN THAILAND

1. Lateral scales in rows pointing backwards and downwards 2
   Lateral scales in rows pointing backwards and upwards 3
2. Dorsal scales keeled; ventrals strongly keeled, three to five times larger than the dorsals. The six to ten dorsal scalerows pointing backwards and upwards; lateral scales point backwards and downwards; gular scales smaller than ventrals; color generally green in life but capable of changing; 60 to 100 scales around the body ..... *cristatellus*
   Dorsal scales smooth or feebly keeled, larger than the median ventrals, all rows pointing backwards and downwards; gular scales as small or a little smaller than ventrals; color generally light brown around body ..... *floweri*
3. No fold or pit with small scales in front of shoulder; two spines above the tympanum; throat and chin with longitudinal dark streaks; color generally fawn with brownish or blackish marks or bars; 35 to 52 scales around body at middle ..... *versicolor*
   A fold or pit with small scales in front of shoulder 4
4. No postorbital spine present; the fold in front of shoulder oblique, with fine granular scales in the fold; a cream stripe along upper lip extending well onto shoulders; male with three to five large reddish brown or dark brown spots on sides; 48-52 scales around body, *mystaceus*
   A postorbital spine present 5

5. A large well-defined postorbital spine (or two small groups of spines) above tympanum on occiput; a diagonal or angular fold on shoulder about a shallow pit, its bottom covered with fine granular scales, deep black in color; 40-48 scales around middle of body, *emma emma*

A very low postorbital tubercle or spine; two low tubercles or spines above tympanum; 60-65 scales around the middle of body; a high nuchal crest. ..... *emma altacristatus* *

Calotes cristatellus (Kuhl)

FIG. 50

Agama cristatella Kuhl, Beitr. Zool. vergl. Anat., vol. 1, 1820, p. 108 (type-locality, not designated).

Bronchocoela cristatella: Kaup, Isis, 1827, p. 619; Duméril and Bibron, Erpétologie générale . . ., vol. 4, 1837, p. 395 (East Indies).

Calotes cristatellus: Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 316; Ann. Mus. Civ. Genova, ser. 2, vol. 6, 1888, p. 318; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 134; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 70; Flower, Proc. Zool. Soc. London, 1896, p. 871; *ibid.*, 1899, p. 639; Baumann, Zoolog. Jahrb., System., vol. 34, 1913, p. 266, fig. B; de Rooij, The reptilia of the Indo-Australian Archipelago, vol. 1, 1915, pp. 121-122, fig. 53; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 2, Aug. 1914, p. 130; *ibid.*, no. 3, Mar. 1915, p. 154 (Sai Yoke district); *ibid.*, vol. 2, no. 1, June, 1916, p. 54; *ibid.*, no. 2, Dec. 1916, p. 155 ("Bangnara" [= Narathiwat] and Klong Bang Lai, "Patiyu" [= Chumphon]); Bull. Raffles Mus., no. 3, Apr. 1930, p. 27; Journ. Federated Malay States, vol. 10, 1922, p. 269.

Agama guttorosa Merrem, Tentamen systematis amphibiorum, 1820, p. 51 (type-locality, "America" based on Seba, vol. 1, p. 1, pl. 89, figs. 1-2).

Agama moluccana Lesson, Voyage Coquille; Reptilia, 1830, pl. 1, fig. 2 (type-locality?).

Bronchocoela burmana Blanford, Journ. Asiat. Soc. Bengal, vol. 48, 1878, p. 127 (type-locality, Tavoy, Burma).

Diagnosis: Scales on sides pointing backwards and downwards; no skinfold or pit anterior to shoulder. The hind limb reaches to eye or farther; fourth finger as long as fifth toe; six to ten upper scalerows pointing backwards and upwards; strong nuchal crest in male; dorsal crest lower. Snout to vent, 130 mm.; tail, 440. Body much compressed.

Description of species (from No. 134 ♀ La Doo Tin Mine near Bendang Stah, Yala): Body much compressed; rostral very small about one third of the size of mental, bordered laterally by labials, and behind by three postrostrals, separated from nasal by three or four scales; nasal angular separated from labial series by one scalerow; canthal edge sharp, scales relatively small, continuous with supraciliaries; frontal area concave continuous with a concave

* The question as to whether this should be regarded a subspecies or a full species is not fully decided. There seems to be a considerable hiatus between their ranges; they are here regarded as subspecies.

FIG. 51.—*Calotes versicolor* (Daudin). No. 349, Songkhla, Songkhla, Thailand. Snout-vent length, 97; tail, 262 mm.

area between orbits; scales on snout keeled or ridged, subequal, a little smaller than keeled scales above orbits; two or three enlarged scales in occipital region; a somewhat enlarged scale at posterior end of supraciliary border followed by a series of three compressed scales; tympanum large superficial, its diameter (4.5 mm.) half diameter of orbit (9 mm.); supralabials, 10-11 with a longitudinal keel, and a slight elevation on labial edge; 10-11 infralabials, a distinct keel and an elevation on labial border giving scales a troughlike appearance. Mental with a labial border much greater than that of rostral, bordered behind by a pair of chinshields separated by a scale; these followed by a diverging series of larger scales, that diminish in size and become similar to adjoining scales. Scales on back of head, on neck, and front of shoulders, small, high, compressed; scales farther back are lower, elevated parts are keels which may be higher at one end of the scale than at the other; keeled scales on back and sides for most part directed backwards and downwards, except six or eight upper rows which are directed backwards and upwards; a nuchal crest composed of about ten flattened scales reaching their greatest height (5 mm.) at middle of series; dorsal crest very low serrate; scales on tail larger, longitudinally keeled, the series pointing directly backwards; scales on chin strongly keeled, larger than those on head above; a slight nuchal pouch in males; ventral scales much larger than dorsal and laterals, strongly keeled, somewhat mucronate, keels parallel; subcaudal scales moderately keeled; scales on arms and legs enlarged, keeled.

Arms and legs slender, elongate, leg reaching a little beyond eye; third and fourth fingers subequal; fourth toe much longer than third; subdigital lamellae with double keels, rarely with three keels. About 90 scales around body; small fold from jaws runs back to shoulder.

Color in life: Whole body green, nearly uniform; this changed in a few minutes, showing a tail banded with gray-brown and ultramarine; two large chocolate brown patches on sides of rump; in fixative dark blackish brown with light brown transverse bars across back; proximal part of tail similarly marked, light and darker bands of nearly same width; distal bands blackish brown and ultramarine the dark bands several times wider than the light. Chin yellow-green; throat bluish especially laterally; venter lavender; underside of arm cream, of leg, bluish white.

Measurements in mm. of Nos. 1349, and 1534, respectively: Snout

to vent, 110, 122; tail, 374, 454; width of head, 19, 20.5; length of head, 33, 38; snout to arm-insertion, 43, 45; axilla to groin, 56, 68; arm, 55, 63; leg, 93, 104.

Variation: The series of compressed scales back of the supraciliary border vary in size, being usually more evident in males; the number of scalerows about the body at the middle varies (in the entire range) from 60 to 100 strongly suggesting subspecific differentiation in certain of populations. In Thailand the variation is less than ten in specimens I have examined. However, Malcolm Smith states that specimens from the extreme north (Sai Yoke district Kanchanaburi and Patiyu, Chumphon have 60-62 scales) which is a difference of 30 or more scalerows. I have not examined specimens from these localities.

Distribution: In Thailand the species is confined to the peninsular area, and the adjoining mainland north of the peninsula. It has been taken in Kanchanaburi, Chumphon, Narathiwat, Yala, and Pattani provinces, but may be expected in all provinces in the peninsula. It is wide-spread in Malaya.

Remarks: This species changes color very rapidly. One may see a brilliant green lizard one minute and a short time later it may turn almost completely black. If such a specimen is left undisturbed for a few hours in the dark it may resume the brilliant green coloration.

The eggs are oval; oviductal eggs measure about 30 by 12 mm.

Calotes floweri Boulenger

Calotes floweri Boulenger, The fauna of the Malay Peninsula from the Isthmus of Kra to Singapore; Reptilia and Batrachia, 1912, p. 70 (type-locality, Siam and the Malay Peninsula [restricted to Chanthaburi Thailand by Taylor and Elbel]); M. Smith, Journ. Federated Malay States Mus., vol. 10, 1922, p. 269; Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 54; The fauna of British India including Ceylon and Burma . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 186-187; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1097-1098 (type-locality restricted).

Calotes microlepis: (not of Boulenger) Boulenger, Journ. Federated Malay States Mus., vol. 3, 1908, p. 66.

Diagnosis: Forehead flattened with an inverted Y-shaped series of enlarged scales; dorsal and lateral scales keeled, pointing backwards and downwards; 48 to 64 scales around body; nuchal crest composed of erect, compressed spines. Head large, its length twice its width.

Description of species (from EHT-HMS No. 31717): Head relatively narrow, its length twice its width; frontal region flat, dis-

tance between edge of orbit and nostril slightly greater than diameter of orbit. Rostral wide, low, bordered behind by two labials and five postrostrals; a group of enlarged scales form an inverted Y-shaped figure, scales forming branches of the Y, continuous with two enlarged "semicircular" scale series on inner border of supraocular region, separated from each other by three scalerows; at level of occipital scale (bearing "pineal eye") a transverse row of slightly elevated scales, with a few enlarged scales on each side of occipital region; scales in temporal regions unequal with one differentiated series from eye to above tympanum. Twelve supralabials, last three not clearly differentiated; eleven infralabials; mental narrow, as wide as long, followed by two enlarged rows of six scales each and except for first, separated from each other by one row of scales anteriorly, to five rows posteriorly. About 64 scales in a transverse row around body, dorsal and lateral scales arranged in longitudinal rows that point backwards and downwards; dorsal scales subequal in size in more or less distinct transverse rows, larger than those on the venter, but the scales on venter more strongly keeled.

Body strongly compressed; legs slender; a gular pouch scarcely discernible; tail definitely compressed but swollen and serrate at base, median scales somewhat larger than the rest.

Color: Generally light brown above; four indefinite darker brown marks present on dorsum, first between shoulders; tip of head darker, with radiating dark streaks from eye; venter very light brown with or without dark marks; tail lighter than body, barred with bands of brown and light tan.

Measurements in mm.: Snout to vent, 98; tail, 180 (from type description).

Variation: The supralabials vary between eight and twelve in number. The nuchal crest which in both sexes is composed of from six to nine erect compressed spines, is lower in females. The dorsal crest forms a serrated ridge in the male but is absent in the female. In the male the tail is thickened and swollen at the base.

Distribution: The species was originally discovered in mountains near "Chantaboon" = Chanthaburi, southeastern Thailand at an elevation of about 1500 ft. The species has also been taken in Cambodia at 3000 ft. and in Malaya at from 6000-7000 ft. elevation.

Remarks: The specimen described has scales smaller and in larger number than the type specimen described by Boulenger. In

consequence it resembles somewhat the species *C. microlepis* (scalerows around body 65-72), described by Boulenger from southern Burma. It is possible that *microlepis* and *floweri* are subspecies of a single species. Sufficient material is not available to determine this. The specimen here considered may be somewhat intermediate in character between the two.

Calotes versicolor (Daudin)

FIG. 51

Agama versicolor Daudin, Histoire naturelle générale et particulière des reptiles, vol. 3, an X = 1802, pp. 395-397 (type-locality [based on Kuhl] Pondicherry, designated by Malcolm Smith).

Calotes versicolor: Jerdon, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 470; Blyth, Journ. Asiat. Soc. Bengal, vol. 22, p. 649; Günther, The reptiles of British India, 1864, p. 140; Theobald, Journ. Linn. Soc., vol. 10, Zoology, 1868, p. 33; Anderson, Proc. Zool. Soc. London, 1872, p. 381; Blanford, Zoology of Eastern Persia, 1876, p. 313; Anderson, Anatomical and zoological researches and zoological results of the Yunnan Expeditions . . . 1878-79, p. 805; Murray, The vertebrate Zoology of Sind, 1884, p. 367; Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Camboge, 1885, p. 89; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 321; The fauna of British India . . . Reptiles and Batrachians, 1890, p. 135, fig.; Flower, Proc. Zool. Soc. London, 1899, p. 639; Annandale, Proc. Zool. Soc. London, 1900, p. 858; Journ. Asiat. Soc. Bengal, vol. 73 Suppl. 1904, p. 18; M. Smith and Gairdner, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 3, Mar. 1915, pp. 130, 154 (Rat Buri, Petchaburi); M. Smith, *ibid.*, vol. 2, no. 1, 1916, p. 54; *ibid.*, no. 2, 1916, p. 155 (Narathiwat, Pattani, Nakhon Si Thammarat); *ibid.*, vol. 4, no. 2, p. 96; Mell, Arch. Naturges., Bd. 88, 1922, p. 112; Chabanaud, Mission Babault résultats scientifiques, reptiles et batraciens, 1922, p. 4, pl. 1, fig. 1; Proctor, Journ. Bombay Nat. Hist. Soc., vol. 29, 1923, p. 123; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 415; Jouquet, Journ. Bombay Nat. Hist. Soc., vol. 33, 1929, p. 452; Deraniyagala, Ceylon Journ. Sci., sec. B, vol. 16, 1931, p. 150; Brongersma, Mem. Mus. R. Hist. Nat. Belgique, vol. 5, 1931, p. 19; M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 189-193, fig. 54; Baldauf, Copeia, 1949, pp. 289-290; Randow, Aquar. Terrar. Z. Stuttgart, vol. 5, 1952, pp. 185-187; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1098-1099 (Rat Buri, Kanchanaburi, Chaiyaphum, Nakhon Si Thammarat, Rayong, Phatthalung and Loei); Mertens, Aquar. Terrar. Z. vol. 7, 1954, fig. (Pakistan); Leviton, Myers and Swan, Occ. Papers Nat. Hist. Mus. Stanford Univ., no. 1, 1935, pp. 1-18, Deraniyagala, Spolia Zeylanica, vol. 28, 1, pp. 7, 16.

Diagnosis: Head relatively short; scales on the sides of body pointing backwards and upwards; no fold in front of shoulder; two spines (or groups of spines) above tympanum; light brown, fawn or grayish with darker markings; throat and chin with longitudinal darker marks that are continuous with radiating lines from eye; a dim median dark line on venter; moderate nuchal and dorsal crests continuous, of lanceolate compressed spines, the size diminishing gradually posteriorly; base of tail in males thickened, scales larger and thicker than in females.

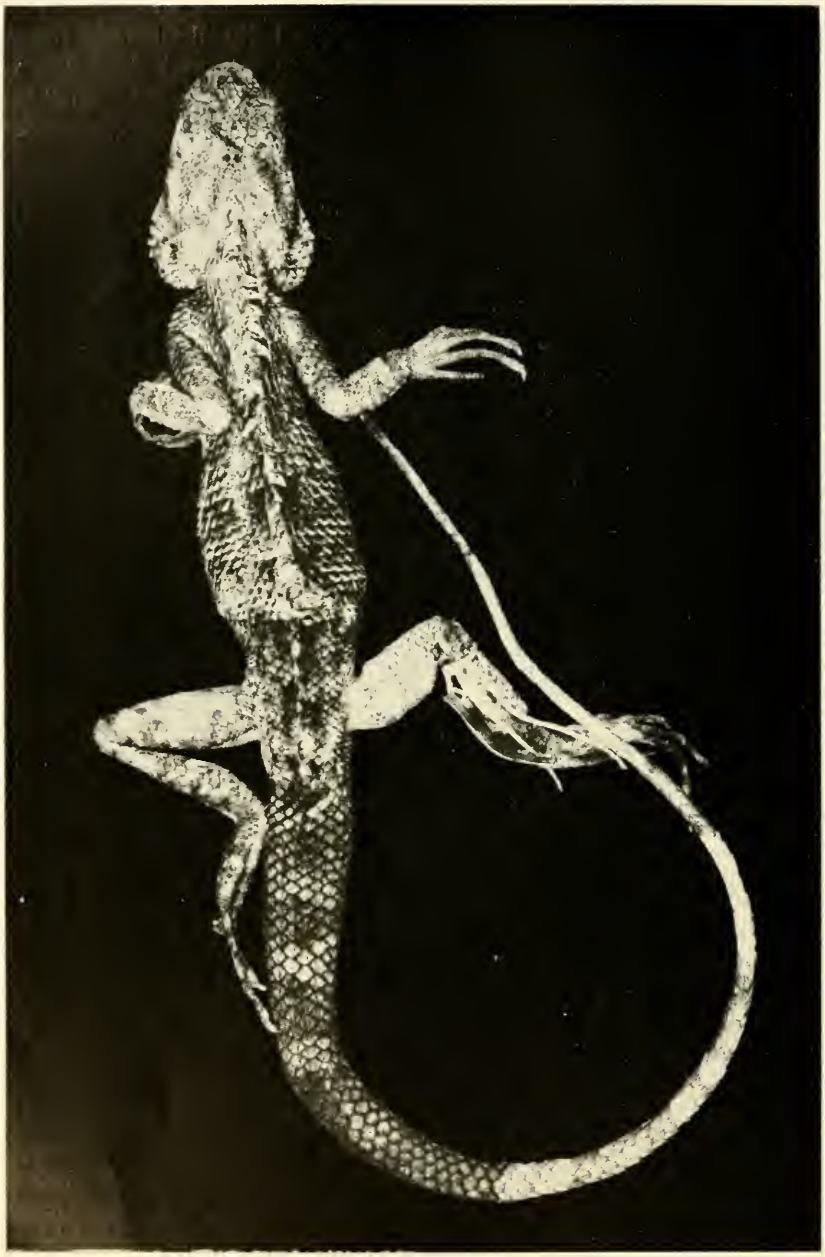


FIG. 50.—*Calotes cristatellus* (Kuhl). EHT-HMS No. 205 Ulu Langat Forest Reserve Kajang, Selangor Malaya. About natural size.

Description of species (from No. 348, Songkhla, Songkhla): Head not or scarcely concave in frontal area; rostral small, about one and one-third times as wide as high (rarely larger), bordered by two labials and three postmentals; nasal with nostril directed outward, separated from rostral by two scales; scales on head varied in size, smooth; median occipital scale (with pineal eye) enlarged; two separated spines, or groups of spines above tympanum; jaws swollen (in male); tympanum slightly sunk, about one half of diameter of eye; canthal and supraorbital edge sharp; ten or eleven supralabials; ten infralabials; mental small, wider than rostral, and larger; a pair of narrow chinshields touching labials each followed by a row of three or four enlarged scales, none touching labials; orbital diameter less than length of snout; gular scales mucronate distinctly larger than ventrals, the scalerows directed mesially; dorsal and lateral scales not keeled; ventrals, keeled and mucronate; basal part of tail swollen, scales keeled and mucronate, basal scales thickened; no caudal ridge or crest; nuchal crest continuous with dorsal, the highest scales about five millimeters high; dorsal crest terminates at base of tail; third and fourth fingers subequal, with 21 scales on their under-surface each with two projecting spines; fourth toe much longer than third with 26 scales similar to preceding scales on finger; leg reaches to near back edge of orbit; 46 scales in a row around body at middle.

Color: Variegated brown and dark olive the latter forming six or seven darker marks on back and more or less connected with an indefinite reticulation on sides; many of the scales with whitish or cream-colored edges suggesting indefinite lighter bars; tail barred with light and darker olive, markings growing very indefinite distally; in basal part of tail skin between scales blackish.

Measurements in mm.: Snout to vent, 98; tail, 260; snout to arm-insertion, 35; axilla to groin, 45; width of head, 24 at tympanum, at temporal region, 18; length of head, 33; arm, 45; leg, 73.

Variation: Some specimens may have a narrow greenish-white dorsolateral line which interrupts the transverse dark markings. In some specimens the darker bands are more or less continuous under the tail. Occasional specimens have the head almost black with black lines on supralabials and infralabials. It is possible that these variations may occur in the same individual at different times.

Distribution: The species is widespread in Thailand and prob-

ably it occurs in all the provinces. It is common in the city of Bangkok in gardens and trees and along fences. Outside of Thailand the species ranges from Afghanistan, India and Ceylon east to Hong Kong, Indo-China, Malaya, and Sumatra.

Remarks: Within this great range some of the variants differ sufficiently to be regarded as subspecies. Whether the Thailand form is typical cannot be ascertained at this time. One Indian form reaches a size nearly a half larger than the typical-sized adults of Thailand.

Aside from the provinces from which this species has been reported, I have taken it also in Phra Nakhon, Ayutthaya, Khon Kaen, Nong Khai, Ubon, Sara Buri and Nakhon Ratchasima.

Annandale reports a remarkable behavior in courtship in one form of this species.

"The males are pugnacious and change color as they fight. In courtship the male approaches the female concealed in the foliage. He chooses a conspicuous station and advances towards the female. He is now a pale yellowish flesh color with a conspicuous dark spot on the gular pouch which is fully distended. He stands upright raising the fore-part of the body as high as possible, nodding his head solemnly up and down. As he does this the mouth is opened and closed rapidly and repeatedly."

Calotes mystaceus Duméril and Bibron

FIG. 52

Calotes mystaceus Duméril and Bibron, Erpétologie Générale . . . vol. 4, 1837, p. 408 (type-locality, Burma); Blyth, Journ. Asiat. Soc. Bengal, vol. 21, 1852, p. 354; Theobald, Descriptive catalogue of the reptiles of British India, 1876, p. 106; Boulenger, Catalogue of the lizards in the British Museum, 2nd ed., vol. 1, 1885, p. 325; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 138; Annandale, Journ. Asiat. Soc. Bengal, vol. 73, 1904 (2) Suppl., p. 18; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, March 1915, no. 3, p. 154 (Sai Yoke district); *ibid.*, no. 4, Dec. 1915, pp. 256-257 (Paknampo; Hua Hin); *ibid.*, vol. 2, no. 1, June 1916, p. 54 ("Common and widely distributed extends as far south as Bangsaphan Lat. 11° 13′"); Proc. Zool. Soc. London, 1921, p. 429; Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, p. 295 (Chiang Mai); M. Smith, The fauna of British India, Ceylon and Burma . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 197-199; Romer, Journ. Bombay Nat. Hist. Soc., vol. 48 (2), 1949, pp. 374-376.

Diagnosis: Scales on the sides of the body pointing backwards and upwards; an oblique fold and triangular pit in front of shoulder covered by small granular scales; dorsal scales larger than ventrals; no postorbital spine; fourth toe distinctly longer than third; 48-58 keeled scales round middle of body; nuchal and dorsal crests continuous; a white stripe on upper lip and side of head passing through tympanum to shoulder.

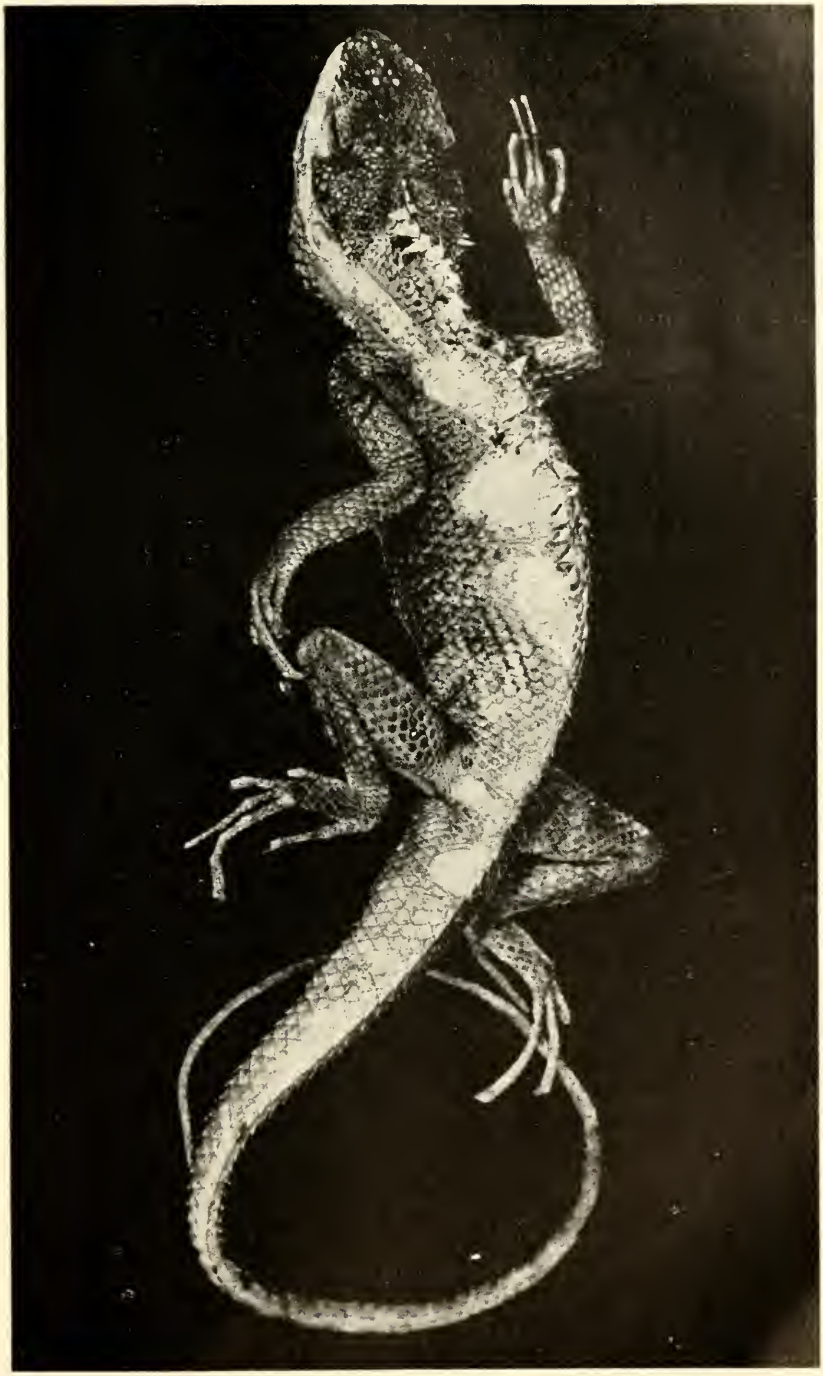


FIG. 52.—*Calotes mystaceus* Duméril and Bibron. No. 1486, near Kanchanaburi (km. 111). Actual length, snout-vent 110; tail, 228 mm.

Description of species (from No. 1481 Kanchanaburi province): Large species, area back of jaw-angle swollen, length of head about one and a half times its breadth; snout longer than orbit; rostral small, bordered by five postrostrals and laterally by a labial; frontal region shallowly concave; nostril in a single somewhat craterlike scale, directed outwards and somewhat backwards, separated from rostral by a scale; one or two larger scales above nasal; a longitudinal row of four bluntly ridged or keeled scales on middle line of snout; a patch of somewhat larger scales above on eyelids and another area on each side of occiput, the scales rough, some more or less keeled; canthus rostralis distinct, canthal scales more or less continuous with supraciliary series; supralabials 12-12, separated from small scales of orbit by three scalerows; an irregular row of larger scales from orbit to above tympanum; latter distinct, superficial, its diameter nearly half length of orbit; in area above tympanum two groups of scales consisting of a median elevated spine surrounded by three or four smaller spines; infralabials, 10-10; mental small, triangular, its labial border much smaller than rostral border; mental bordered by a pair of chinshields, not in contact, each followed by two enlarged scales, the series diverging, only first touching infralabials; scales on chin and throat rather large, keeled, mucronate or terminating in a spine; a strong nuchal crest continuous with a dorsal crest, latter continuous to end of body, the scales growing smaller posteriorly; median dorsal caudal scales strongly keeled making a low caudal crest; dorsal and lateral scales keeled, the rows pointing upwards and backwards; caudal scalerows directed backwards and slightly upwards; scales on venter smaller than dorsals, keeled, the keels parallel; subcaudal scales keeled, slightly smaller than lateral caudal scales.

Arms moderate, fourth finger longer than third; leg long, the leg brought forward toes reach tympanum; fourth toe distinctly longer than third; lamellae under digits with double keels, the keels becoming spinose anteriorly.

Color: This specimen, a large male, has head completely black except for cream stripe beginning somewhat back of nostril, covering supralabials and four scalerows; crossing tympanum it terminates on neck; sides of body dark olive the color covering arms and legs above; three rusty-brown spots on sides reaching up to dorsal crest; base of tail light olive, distal part dimly banded in dark olive and olive-gray; chin and throat deep black; venter light olive under limbs; basal part of tail dirty white.

Measurements in mm. (Nos. 1481 and 1485): Snout to vent, 132, 122; tail, 278, 233; width of head, 32, 30; length of head, 45, 40; snout to arm-insertion, 48, 47; axilla to groin, 63, 55; arm, 54, 56; leg, 86, 74.

Variation: A second specimen, a male, taken in the general vicinity of Kanchanaburi at the same time that the described specimen was taken, differs very markedly in color. However, the stripe on the head and neck and the three brown spots are in evidence. The area about the eye is black, as are the infralabials and part of the scales on chin and throat.

The head is bluish olive, and the anterior crest-scales are blue. The tail and part of the sides are fawn, while the venter is yellowish cream. The tail shows no trace of bands.

The highest part of the nuchal crest measures eleven millimeters; of the dorsal crest ten millimeters. The crest-scales in the second specimen measure nine and seven respectively. In all specimens the body is compressed.

Distribution: In Thailand I have taken specimens in the following provinces: Chiang Mai, Loei, Nong Khai, Udon Thani, Sara Buri, Khon Kaen, Kanchanaburi and Phet Buri.

It has been reported or collected in Nakhon Pathom, Rat Buri, and Chaiyaphum.

Taylor and Elbel have reported the species from Nakhon Si Thammarat but this I now believe to be an error despite the label the specimen bears.

Remarks: Courtship and egg laying are described in the introduction to the genus p. 884.

Calotes emma emma Gray

Fig. 53

Calotes emma Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 244 (type-locality *ex errore* "Afghanistan"); Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, pp. 413, 647; Günther, The reptiles of British India, 1864, p. 144; Theobald, Journ. Linn. Soc., vol. 10, Zoology, 1868, p. 38; Anderson, Anatomical and zoological researches and zoological results of the Yunnan Expeditions; Reptilia and Amphibia, 1879, p. 806; Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 324, pl. 25, fig. 1; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 137; Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 155; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 73; Flower, Proc. Zool. Soc. London, 1889, p. 641; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 54 ("commonly distributed but not found in Bangkok"); *ibid.*, no. 2, 1916, p. 155 (Narathiwat, Pattani, and Nakon Si Thammarat); The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 195-197, fig. 55; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1099-1100 (Loei, Sakon Nakhon, Phattalung, and Nakhon Si Thammarat provinces).

FIG. 53.—*Calotes emma emma* Gray. No. 1341, La-Doo, Tin Mine Benang Stah, Yala. Actual snout-vent length, 99 mm.; tail, 261 mm.

Diagnosis: Scales on the sides of the body pointing backwards and upwards; a fold or pit on front of shoulder paved with minute black scales; dorsal scales larger than ventrals; a postorbital spine; 49-65 keeled scales round body; nuchal crest high in males.

Description of species (from No. 237 Coffee Camp, Na Bon Nakhon Si Thammarat): Head moderately large, its length about 1.5 times its width; rostral twice as wide as long bordered by two nasals and four postrostrals, outer ones separating nasals and rostral; scales on head unequal, keeled or rugose; two enlarged scales on frontal area; one or more enlarged supraocular scales; an elongated spine behind supraorbital edge, its length one half (or more) of diameter of orbit; a large spine on occipital region, surrounded by somewhat shorter spines, and another similar spine above tympanum; tympanum large superficial its length about half diameter of orbit; a sharp, slightly overhanging canthus rostralis; nine to eleven supralabials, eight or nine infralabials; mental narrowed behind, its labial border much smaller than that of rostral; scales on chin strongly mucronate; scarcely a trace of a gular sac; curving fold of skin in front of shoulder (sometimes angular) bordering a triangular "pit" or area covered with minute black scales; high nuchal crest of compressed scales with lower spines closely applied at their bases; this crest continues with a dorsal crest of much lower spines proportionately wider at their bases than those in the nuchal crest.

Scales on dorsum and side subequal; those on flanks a little smaller, strongly keeled and mucronate the scales pointing upwards and backwards except those low on flanks which point down and backwards; scales on dorsum equal to or larger than ventral scales; latter rather strongly mucronate; 46 scales about middle of body; tail swollen somewhat at base but scales not thickened; most other caudal scales keeled and mucronate.

Limbs well developed, fourth finger a little longer than second, with a row of 20 scales below, each with two spines; fourth toe longer than fourth finger, with 25 scales on undersurface, all with two forward-projecting short spines; hind leg reaches eye. Most scales with a small hairlike process emerging from posterior end of keel or just below the mucrone.

Color in life: Head dark red-brown tending to become reddish or pinkish posteriorly and on neck the red extending as far as 12th spine in crest; a black line from eye to above tympanum; lips and area in front of tympanum reddish; throat blackish mixed with red flecks; body yellowish brown to fawn with six transverse

marks, each tending to divide near mid-dorsal line and on middle of side. Tail banded with dark olive and dull gray-buff; some yellow coloring in groin; arms mottled with olive; legs strongly barred above with olive or olive-brown; venter, subcaudal area, and undersurface of limbs grayish, often with cream flecks.

Measurements in mm.: Snout to vent, 97; tail, 249; snout to arm-insertion, 37; axilla to groin, 47; width of head, 21.5; length of head, 32; arm, 49; leg, 75.

Distribution: The species occurs in peninsular Thailand. It has been taken in Pattani, Yala, Narathiwat, Trang, and Nakhon Si Thammarat.

Remarks: Females are less brilliantly colored, but the black shoulder spot, the lip area, and the transverse markings on back and tail are similar in the two sexes. Most young specimens of both sexes have the chin and neck displaying black longitudinal striations.

This species is common in southern Thailand especially in Trang and Nakhon Si Thammarat. In the month of November a period of much rain, I was able to find only two sizes of young, some with a snout-vent measurement of 32-48 mm., the smallest recently hatched; and another group that measured 65-74 mm., snout to vent. Only one adult female in half a months collecting was seen. During the month of May almost all of the specimens seen in this area, and they were ubiquitous, were fully adult males and females. A large number could easily have been taken. One presumes that most adults find cover and keep in hiding during the rains.

Calotes emma alticristata Schmidt

Calotes alticristata Schmidt, Amer. Mus. Novitates, no. 175, 1925, p. 2; Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 482, fig. (type-locality, Yunnan-fu); M. Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 197, under synonymy of *C. emma.*

Diagnosis: A form related to *Calotes emma emma* having a tubercular scale at end of the supraciliary edge, a longer and stronger nuchal crest and smaller dorsal scales; 10 to 15 more scales around the middle of body, and reaching a larger size (120 mm. snout to vent).

Description of species (from No. 36, from "near Whe Tat, northern Chiang Mai province"): Rostral twice as wide as high followed by two labials and five postrostral scales; nasal with nostril directed outward and somewhat backward, separated from rostral by a single scale; scales on snout forming an indistinct, inverted Y-shaped

group on snout and frontal area; some enlarged elongate scales in supraocular area; head scales variable in size, keeled or rugose; a tubercular scale back of supraciliary edge; canthus distinct, overhanging loreal region somewhat; tympanum large, superficial, slightly more than half diameter of orbit; a small spine in occipital region, and one above tympanum; nine or ten supralabials; ten infralabials; mental small, its labial border less than that of rostral, followed behind by two labials and two large postmentals, the latter separated by a narrow scale; each followed by two large chinshields, one behind the other. Gular scales much larger than ventrals; a high nuchal crest more or less continuous with dorsal crest; an angular fold in front of shoulder enclosing a black triangular spot; three or four enlarged scales between eye and upper edge of tympanum; body strongly compressed; scales on back in rows pointing backwards and upwards; lateral rows on flanks pointing backwards; third and fourth fingers equal; leg reaching to orbit; fourth toe with 29 transverse scales each with two spines or mucrones pointing down and somewhat forward; tail not or but slightly compressed; a slight gular pouch present.

Color: Light olive to gray-brown, top of head somewhat darker brown; a dark line in loreal region continued back of eye to above tympanum; upper and lower lip creamy white, the color extending back to below tympanum; chin and gular area grayish with black on skin between scales; throat blackish; dorsum with a series of six bands, more or less broken dorsolaterally by an indefinite light line, the bands each including a light spot on middle of back, and laterally forked to surround a lighter area. Tail banded gray and blackish.

Measurements in mm.: Snout to vent, 120; tail, 289; snout to arm-insertion, 49; axilla to groin, 60; width of head, 25; length of head, 36; arm, 50; leg, 83.

Distribution: Known in northern Thailand (Chiang Mai) and in southern China.

Genus Aphaniotus Peters

Aphaniotus Peters, Monatsb. Akad. Wiss. Berlin, 1864, p. 385 (type of genus, *fuscus*).

A small agamid, snout to vent, 72 mm. or less; body compressed; tympanum hidden; dorsal scales small, intermixed with enlarged scales, some of which are in rows; a small nuchal crest; lacking femoral and preanal pores; a small gular pouch; toes long, fifth as

long or longer than first; arms and legs very long the leg reaching snout or beyond.

Two species are recognized of which only one, *A. fuscus*, enters our territory.

Aphaniotus fuscus (Peters)

FIG. 54

Atocryptis (Aphaniotus) fusca Peters, Monatsb. Akad. Wiss. Berlin, 1864, p. 385 (type-locality, "Malacca"?).

Aphaniotus fusca: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 274; Laidlaw, Proc. Zool. Soc. London, 1901, vol. 1, p. 307; Boulenger, Journ. Federated Malay States Mus., vol. 3, 1908, p. 65; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 64; de Rooij, The reptiles of the Indo-Australian Archipelago, Lacertilia, Chelonia, Emydosauria, 1915, p. 90; Sworder, Journ. Mal. Brit. Roy. Asiat. Soc., vol. 7, 1929, p. 327, text figs.; M. Smith, Bull. Raffles Mus., no. 3, 1930, p. 23 (Pattani).

Aphaniotis floweri Werner, Zool. Jahrb., Syst., vol. 13, 1900, p. 468.

Diagnosis: A median line of enlarged scales on snout; supraorbital region with enlarged keeled or ridged scales; legs elongate, fourth toe reaching several millimeters beyond tip of snout; tympanum hidden, the area with one enlarged scale; snout about equal to length of eye; a row of enlarged keels on each side of midline, separated by seven scalerows.

Description of species (from EHT-HMS. No. 226, King George National Park, Kuala Tahan): Rostral vertical, a little more than three times as long as high; front face somewhat concave, with a small transverse ridge near mouth, in contact laterally with first supralabials, and bordered behind by seven scales, median largest; beginning with this scale, there follows a series of five scales in a line then two at terminus; nasal angular, elevated, craterlike, separated from rostral by one scale; an enlarged supranasal; canthus rostralis sharp; canthal scales continuous with supraciliary scales, 12 in all; supraocular region with six rows of enlarged scales those mesiad largest; occipital scales irregular, enlarged, keeled, the keels directed in various directions; eight supralabials each with a slight keel except first; mental triangular with a labial border equal to that of rostral; five distinguishable chinshields none in contact, first pair borders mental; a row of irregular scales from eye to above tympanum.

Scales on head generally pyramidal or conical; ten rows between the two largest series on supraocular areas; scales on body small, elevated, subimbricate; a row of enlarged keeled scales on each side of the back extending to level of legs. A second row indicated anteriorly on side of neck and shoulders; scales on chin and throat

smaller than scales on venter; ventrals imbricating, strongly keeled, the keels terminating in elevated mucrones; scales on arms, legs and tail enlarged, keeled (sometimes mucronate), imbricate; 27 scales under longest toe (counting those on free portion); fifth toe longer than first, second, or third; leg reaching beyond tip of

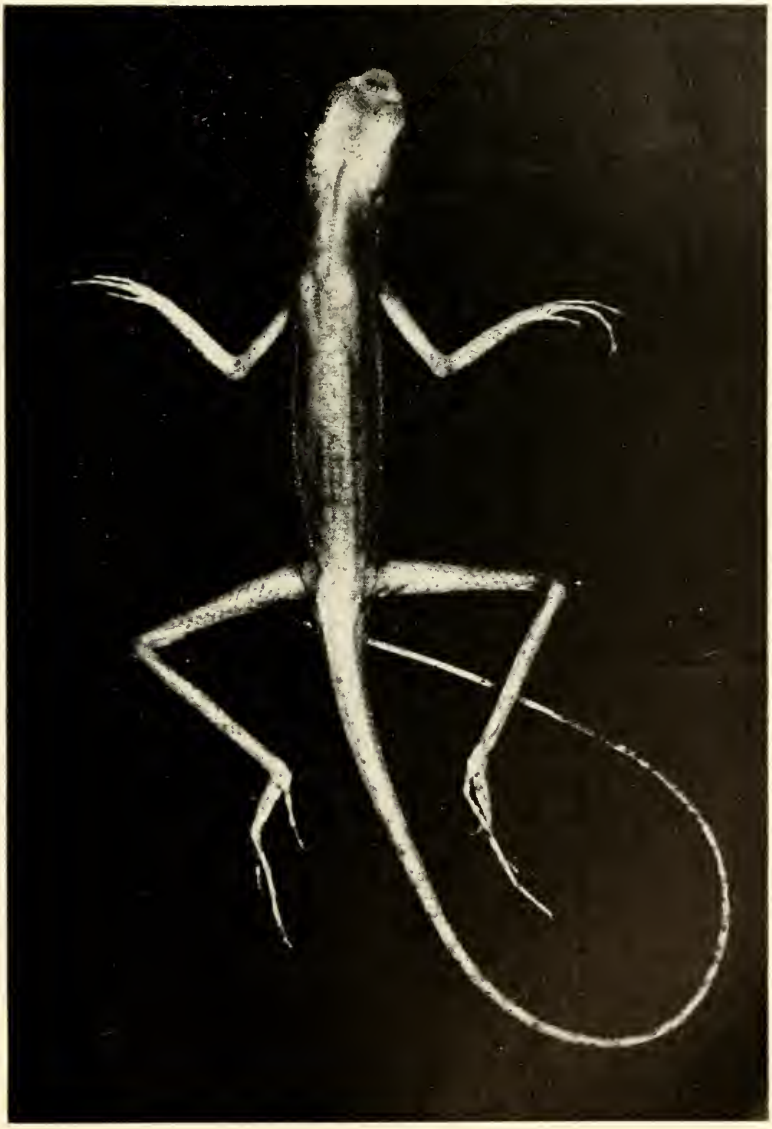


FIG. 54.—*Aphaniotus fuscus* Peters. EHT-HMS No. 226, King George National Park, Pahang Malaya. Actual length, 216 mm.

snout. A small nuchal crest; dorsal crest scarcely distinguishable; tail cylindrical, long and slender.

Color: Head olive-brown above, lighter brown in occipital region; sides of head and chin with a suggestion of bluish-green color; gular pouch black; back nearly uniform dark brown. Arms darker on upper part, lighter on forearm with or without some bands; leg similar, lower leg lighter than upper part with some suggestion of banding; tail with narrow darker and lighter bands seemingly not normally symmetrical; inside of mouth blue.

Measurements in mm.: Snout to vent, 63; tail, 153; width of head, 13; length of head, 16; snout to arm-insertion, 26; axilla to groin, 30.5; arm, 38; leg, 65.

Distribution: In Thailand the species has been taken only in Pattani. I saw two specimens but was unable to capture them at a place near La Doo Tin Mine, Benang Stah, Yala. When I first saw them at some distance I mistook them for young specimens of *Calotes*.

Outside of Thailand the species is known in Malaya, Borneo and the Natuna Islands.

Genus Leiolepis Cuvier

Leiolepis Cuvier, Règne Animal, 2nd Ed., 1829, p. 37 (type of genus, *guttatus*).

Diagnosis: Body rather strongly depressed; no crests; dorsal scales usually small, juxtaposed, conical or pyramidal, and more or less keeled; no distinct gular pouch, but one or two transverse gular folds; femoral pores in both sexes; tail long, somewhat thickened at base, the scales nearly uniform; ventral scales imbricate, subquadrangular forming transverse rows.

Two subspecies are recognized in Thailand: *Leiolepis belliana belliana*, and *L. b. rubritaeniata*. A third form *L. b. guttatus* may also occur in the extreme eastern part of the country.

Key to Three Subspecies of Leiolepis belliana

1. The black edges of spots on back and dorsolateral area form a definite reticulum and lack almost completely a longitudinal or linear arrangement; nine to twelve scales across middle of undersurface of tibia; trace of a lateral stripe above and anterior to leg-insertion, *b. rubritaeniata*

   No dark reticulum on dorsum; lines or rows of spots present 2

2. Twelve or fourteen scales across undersurface of tibia at middle; ventral scales about as broad as two dorsal scales . . . *b. guttulata*

   Seven to twelve scales across undersurface of tibia at middle; ventral scales as broad as three or four dorsal scales . . . . . *b. belliana*

Leiolepis belliana (Gray)

Uromastyx belliana Gray, Zool. Journ., vol. 3, 1827, p. 220 (type-locality, Penang, Malaya, based on Hardwicke's drawing); Illustrations of Indian Zoology, vol. 2, 1834, pl. 72.

Liolepis guttata: Günther, Reptiles of British India, 1864, p. 154.

Leiolepis belliana: Gray, Catalogue of the Lizards in the British Museum, 1845, p. 263.

Liolepis bellii: Cantor Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 41; Swinhoe, Proc. Zool. Soc. London, 1870, p. 240; Boulenger, Catalogue of the lizards of the British Museum, vol. 1, 1885, p. 403; Fasciculi Malayenses, vol. 1; Zoology, 1903, p. 155, pl. 10, fig. 2 (Young); Ann. Mus. Civ. Genova, ser. 2, vol. 5, 1887, p. 477; Flower, Proc. Zool. Soc. London, 1899, p. 642.

Liolepis belliana: Ridley, Journ. Straits Branch Asiat. Soc. no. 32, 1889, p. 191; Boulenger, The fauna of British India . . . 1890, p. 156; Annandale, Proc. Zool. Soc. London, 1900, p. 858; Rec. Ind. Mus., vol. 7, 1912, p. 90; Laidlaw, Proc. Zool. Soc. London, 1901, p. 308; Boulenger, Fauna of the Malay Peninsula . . . 1912, pp. 73-74; Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 4, Dec. 1915, p. 242; *idem.*, vol. 2, no. 1, 1916, p. 54, no. 2, 1916, p. 155; de Rooij, Reptiles of the Indo-Australian archipelago, vol. 1, 1915, p. 136, fig.; Mell, Arch. Naturgesch. Berlin, Bd. 88, 1922, p. 112; Schmidt, Bull. Amer. Mus. Nat. Hist., 54, 1927, p. 416; Copeia, 1928, p. 80.

Leiolepis belliana belliana: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 238-240, fig. 61a and b; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, no. 2, 1958, pp. 1100-1101 (Loei, Kanchanaburi and Sisaket, provinces); Mertens, Senck. Biol., vol. 42, No. 5/6, 1961, pp. 507-510.

Uromastyx reevesii Gray, in Griffith's, Cuvier's Animal Kingdom, vol. 9, 1931, Suppl. p. 62 (type-locality, China).

Leiolepis reevesii: Theobald, Journ. Linn. Soc., vol. 10, Zoology, no. 41, May 30, 1868, pp. 34-35 (Pegu, Tenasserim, Burma).

Uromastyx maculatus Gray, in Griffith's, Cuvier's Animal Kingdom, vol. 9, 1931, Suppl. p. 62 (type-locality ?).

Leiolepis belliana belliana (Gray)

FIG. 55

Diagnosis: Body depressed, lacking a dorsal crest; no spines on head; lateral skin expansible; scales small, mostly keeled; a strong transverse gular fold; tympanum large, superficial; long series of femoral pores separated in pubic region. Tail thickened at base, somewhat depressed. Spotted or lined above, the sides with alternating bars of black and orange.

Description of subspecies (from No. 34399, Yahling, Pattani): Rostral twice as wide as high, bordered by two labials and six smooth postrostrals, two median largest, followed by five strongly keeled scales, outer ones in contact with nasals; nostril in posterior part of nasal, directed somewhat outwards and backwards; canthals not or scarcely differentiated; anterior supraciliary scales overlapping strongly, ridged or keeled; a row of subocular scales, the ones below eye much elongated, more than half length of eye;

scales on snout, frontal, and interorbital areas somewhat enlarged; supraorbital scales and those on occiput very small; no crests; nasal separated from labials by at least three rows of scales; from rostral by one scale; ten or eleven supralabials, last longest; nine infralabials; mental smaller than rostral, partly divided transversely, followed by a pair of postmentals broadly in contact, each of these followed by diverging series of scales, separated from infralabials but parallel to them; tympanum large, slightly sunken, its diameter equal to length of eye-opening; sides of neck plicate with a distinct transverse nuchal fold preceded by another rather indefinite fold; sides of body expansible; all dorsal scales small, keeled; ventrals much larger, about 40 longitudinal rows at middle of body; scales under tibia in nine or ten rows at middle, more than double size of scales under thigh; a series of 18-17 femoral pores separated mesially by 17 pubic scales; caudal scales strongly keeled, in nearly straight transverse rows, growing gradually larger distally; basal portion depressed, widened, then rather suddenly narrowing, terminating in a fine point. Third and fourth fingers subequal, with 20 subdigital scales, each scale with two or three keels; fourth toe with 34 subdigital scales each with two keels and scarcely a suggestion of a third; leg reaches tympanum; at base of third toe (not fifth as stated in Smith, 1935) there are three or four scales with enlarged triangular "spurs."

Color in life: Head olive with darker areas on side; dorsum blackish olive above with black-edged canary-yellow spots usually arranged in lines or fused together to form five lines of the same color; on flanks a series of black and orange bars, black widest dorsolaterally, terminating bluntly or in a point ventrolaterally; throat reticulated black and cream; venter and breast yellowish orange, laterally with dark lines or mottling on breast and very small light olive spots, less obvious on venter; tail yellow-olive at base with numerous spots becoming yellow-brown distally; subcaudal region yellowish; limbs speckled with yellow and with a dark bordered yellow stripe posteriorly on thigh.

Measurements in mm.: Snout to vent, 114; tail, 238; snout to arm-insertion, 42.5; axilla to groin, 54; width of head, 20; length of head, 27; arm, 43; leg, 83.

Variation: A specimen, KUMNH No. 40106 from Srisaget (= ?Sisaket). This specimen measures 139 mm. snout to vent, the tail broken. The specimen a female has retained a color pattern usually regarded as juvenile. The body is blackish above and dorso-

FIG. 55.—*Leiolepis belliana belliana* Gray. No. 1358, Na Pradoo, near base of Bukit Besar, Pattani province. Actual total length, 223 mm.

laterally. A dorsolateral whitish gray stripe extends from the eye to base of tail, the color not solid but each of the scales involved is pyramidal in shape and the anterior face has a black spot partially edged with white. The minute beadlike scales about the base of the pyramids are bluish white. A similarly colored median line bifurcates on neck and runs forward to occiput, partially broken. A gray line from eye above tympanum turns downward and backward, terminating a centimeter anterior to arm-insertion; a diagonal broad blackish stripe from eye to near arm-insertion; a gray lateral stripe broken anteriorly behind and above arm-insertion and extending back to near groin. Scattered gray-white dots on ground color; on arms and legs, throat, and to some extent chin, blackish with fine white dots or marks; vertical bars not indicated on sides; venter and underside of tail unspotted.

Distribution: The subspecies occupies territory probably throughout the whole of peninsular and southern central Thailand. Specimens have been taken in Pattani, Kanchanaburi, Raj Buri, and ?Sisaket.

Remarks: These seemingly prefer sandy soils in which they burrow, and are often common in areas near seashores but not on the shore itself. They move with amazing speed, and are said to sail actually as they take off from a bank. This seemingly is accomplished by the spreading of the lateral skin and increasing the surface. The young hatch from eggs.

Leiolepis belliana rubritaeniata Mertens

FIG. 56

Leiolepis belliana rubritaeniata Mertens, Senck. biol., vol. 42, no. 5/6, pp. 508-509, pl. 28, fig. 2, type-locality Pakjong (Pakchong), 160 km. nordöstlich Bangkok an der Strasse zwischen Bangkok und Korat) Thailand, province of Sara Buri or Nakhon Ratchasima.

Diagnosis: Similar to *L. belliana belliana* in general body form but differs in having the rounded or oval black-edged spots more numerous the black edges forming a distinct dorsal reticulation.

Description of subspecies: (from No. 33800 near Chiang Mai, Chiang Mai province): Rostral nearly three times as wide as high; bordered by two labials and seven somewhat enlarged postrostral scales; scales on snout and interorbital area larger, distinctly keeled, continued back to occiput; seven scalerows between supraocular areas which are largely covered with small equal keeled scales; nasal large separated from rostral by three or two scalerows; can-

FIG. 56.—*Leiolepis belliana rubritaeniata* Mertens. No. 33804, Chiang Mai (city), Chiang Mai province. Actual snout-vent length, 126 mm.; total length, 402 mm.

thals enlarged, elongated, beginning behind nostrils, continuing back to posterior level of supraciliary edge, ridged and keeled in more than a single series. A subocular series of keeled scales begins near nasal, largest of series directly below eye; nine supralabials; eight or nine infralabials distinctly larger than supralabials; mental with a labial border little more than half length of labial border of rostral; mental bordered behind by a pair of chinshields separated from infralabials, which are first of a series of enlarged sublabials, all separated from labials by one, two, or three rows of small scales; scales on chin and throat rounded, moundlike, juxtaposed; two transverse bands of small scales across ventral side of neck, separated by a transverse band of imbricate scales.

Occipital head-scales small; dorsal scales variable, small, tubercular, conical, pyramidal, all juxtaposed, and tending to be arranged in transverse series. Ventral scales much larger, imbricate, subquadrangular, forming transverse series; 16-15 femoral pores present on undersurface of thigh scales on tail in transverse series those below largest, all keeled; terminal two and one-third inches regenerated; scales not arranged in transverse rows; ten or eleven enlarged scalerows on undersurface at middle. Tympanum large, equally as wide as eye-opening; skinfolds on side of neck; loose skin on side of posterior part of abdomen can be spread by action of ribs.

Color and markings: Above with numerous bluish-gray oval spots, their black edges forming a reticulum; an irregular orange lateral stripe almost segmented by eight black diagonal lateral bars. Chin gray, breast with dim darker markings; subcaudal region whitish; reproduced tail pinkish; arms and legs mottled in darker or with numerous light spots; tail with small light dots on dorsal surface.

Measurements in mm.: Total length, 296; snout to vent, 134; tail, 162; width of head, 13; length of head, 32; snout to arm-insertion, 54; axilla to groin, 63; arm, 45; leg, 85.

Variation: The type as figured by Dr. Mertens, differs in having broad black bands on sides separated by narrow orange bands in the region in front of the arm-insertion and in the postaxillary area; these black bars presumably are not on the latter half of body.

Distribution: The subspecies occupies territory in the western and central parts of northern Thailand. Specimens are known from Chiang Mai, Sara Buri and Nakhon Ratchisima provinces.

Physignathus Cuvier

Physignathus Cuvier, Règne Animal, 2nd Ed., vol. 2, 1829, p. 41 (type *Physignathus cocincinus*).

Body more or less compressed; a dorsal, nuchal, and a caudal crest; no distinct gular sac; tympanum partly or completely distinct, superficial; tail compressed, or rounded in some species; femoral pores present.

This genus is chiefly Australian and Papuasian. Only a single Asiatic species is known, this occurring in Thailand and Indo-China. The species has not been taken in the Malay Peninsula.

Physignathus cocincinus Cuvier

Physignathus cocincinus Cuvier, Règne Animal, 2nd Ed., vol. 2, 1829, p. 41 (type-locality, Cochin China); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 6, 1923, p. 50.

Physignathus cochinchinensis: Günther, Reptiles of British India, 1864, p. 153; Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 1, 1885, p. 400; Tirant, Notes sur les Reptiles et les Batraciens de la Cochinchine et du Cambodge; Saigon, 1885, p. 93; Angel, Bull. Mus. Hist. Nat. Paris, 1928, p. 446; Schmidt, Copeia, 1928, p. 78.

Dilophrys mentager Günther, Proc. Zool. Soc. London, 1861, p. 188 (type-locality Chantabun [= Chanthaburi Province], Thailand).

Physignathus mentager: Günther, Reptiles of British India, 1864, p. 153, pl. 15; Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 400; Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Cambodge, 1885, p. 93; Flower, Proc. Zool. Soc. London, 1899, p. 641; M. Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, 1915, p. 241; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 54; Mell, Arch. Naturg. Berlin, Bd. 88, 1922, p. 112; M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 236-238; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, p. 1101 (Sakhon Nakhon).

Diagnosis: Body compressed; nuchal and dorsal crests continuous, caudal crest separated from dorsal by a hiatus; two diverging series of enlarged scales on lower jaw, larger than infralabials; a few scattered enlarged scales behind jaw angle; a nuchal fold; femoral pores in short series; tail strongly compressed; tympanum partly scaled.

Description of species: Snout longer than orbit. Rostral a little wider than high, bordered behind by two supralabials and eight postrostrals; nasals rather small, surrounded by a ring of slightly elevated scales separated from rostral by three scales, from labials by five rows of scales; scales on snout larger than other head scales, about ten rows separating nasals; those on supraocular and occipital regions smaller except for a curved row of enlarged scales defining supraocular areas; a depressed area on anterior part of occiput and

in interorbital region. Cheeks swollen in males; canthal and supraciliary edge rather blunt; a fold across throat; scales in lower part of temporal region, the subocular and loreal areas, larger than those on occiput, the largest ones form a row bordering supralabials; a row of four or five enlarged suboculars; twelve supralabials; eleven infralabials; labial border of mental larger than that of rostral; first pair of chinshields the larger, forming a median suture, each heading a row of eight or nine much-enlarged scales, the rows diverging, two or three of the series touching infralabials scales; scales of chin and throat differ in size, those on sides of throat extending to behind jaw angles, with some enlarged tubercles, the two largest on each side, white in color.

Most of the scales on dorsal surface of head and body juxtaposed, tubercular, ridged, or bluntly keeled; a denticulated nuchal crest arising from a fold of skin continuous with dorsal crest; latter extending to level of leg-insertions, the scales triangular, separated; one or more finely-pointed scales at base of each of nuchals no larger than dorsals; tail with a denticulate caudal crest, the scales triangular touching one another at their bases, terminating at end of basal fourth and followed to tip of tail by two scalerows, with a depression between; lateral scales keeled, small, growing larger ventrally and distally; subcaudal scales enlarged, strongly keeled, ten or twelve rows proximally, usually four distally. Scales on venter imbricate, larger than dorsal scales, more or less keeled and bearing a terminal pit; the scales on limbs imbricate or subimbricate, variable in size, some distally keeled, others tuberculate; third and fourth fingers subequal with 22 lamellae on underside, each with two keels; fourth toe much the longest, with two or three rows of unequal irregular scales below, about 34 scales in each row; scales bordering outer edge of digit with a high compressed keel pointing down; scales at base of third toe especially modified; femoral pore-scales large, four on right side, five on left, the pore situated on posterior edge of scale; tympanum small, much of its surface scaled. The leg reaches almost to nostril.

Color in life: Above, head and body light greenish olive, the enlarged scales on chin bluish bordered with rose-lavender; venter and underside of limbs green with a wash of greenish yellow; anal region and underside of tail yellowish becoming grayish distally; tail gray-green with a series of 12 buff-brown bands beginning about 60 mm. behind vent and continuing to tip of tail, becoming wider and tending to encircle tail distally; the pore-scales cream; underside of hand and foot dirty yellowish white.

Measurements and data on *Physignathus cocincinus*

NUMBER*	746	747	813	748	31728†
Sex	♂	♂	?	♀	?
Snout to vent	198	171	160	158	135
Tail length	532	482	450	.....	351
Total length	730	653	610		486
Head length	67	54	45	45	36
Head width	48	33	31	28	25
Head depth	37	31	27	25	25
Arm	91	82	75	71	61
Supralabials	14–14	13–12	14–14	13–13	...
Infralabials	12–13	10–12	12–13	10–10	.....
Sublabials	11–12	11–11	12–14	11–12	.....
Femoral pores	8–7	6–7	8–8	7–7	.....
Scales under 4th toe	40	36	36–38	34	.....

* From Sanoi River Ubon.
† Sakhon Nakhon.

Variation: The males are larger than females and the crests on neck, dorsum and tail are very much better developed, the individual scales, compressed and longitudinally striated are from 10-12 millimeters in height. There is no complete hiatus between nuchal and dorsal crests but the crest-scales are much reduced in size where the crests meet. There is a distinct break between dorsal and caudal crests. The caudal crest is largely confined to the basal third of the tail, beyond which there are two ridges formed by two scale-rows, which terminate at tip. The femoral pores are better developed and functional in males. (In females the pore may be indicated only by a notch in the pore-scale.) The male reaches a snout-vent length of 250 millimeters with a tail measuring 650. None of my specimens are so large. A male from Sanoi River, Ubon, measures 730 millimeters in total length.

Distribution: In Thailand specimens have been taken in Sakon Nakhon, Ubon, on the stream forming a boundary between Sara Buri and Nakhon Ratchasima, Koh Kut Island, and Klong Menao, Trat (Trad) province. It is probably widely distributed in eastern and southeastern Thailand.

Elsewhere the species is known in Indo-China.

Remarks: The usual type of coloration shows three to five narrow oblique light stripes on each side especially in the young. These may be bluish in life. The underside of the body may be nearly white with patches of blue.

It is said to be an insectivorous species rather than a leaf eating one.

FAMILY VARANIDAE

This family comprises the largest living lizards, those on the island of Komodo, known as Komodo dragons, reaching a length in excess of three meters. The range of the family, which consists of the single living genus *Varanus*, covers almost all of the continent of Africa, Asia south of the Himalayas (including the Arabian Peninsula); the Indo-Australian Archipelago, the Philippines and Australia. They are absent from Madagascar, Tasmania and New Zealand. The family was formerly present in the Western Hemisphere. They appear in the Eocene beds of Wyoming. These constitute a different subfamily, the Saniwinae with the genus *Saniwa*, and possibly also the genera *Paleosaniwa* and *Parasaniwa*.

These animals are catholic in their taste for food and seemingly are willing to eat almost any creature they can bring down. They appear to be very fond of carrion. In Mindanao, Philippines, shallow graves are sometimes opened by these animals at night and the corpses partially consumed. The deed is usually blamed on some forest-devil. The graves of certain peoples living along the Mindanao coasts are covered with masses of coral often three or four feet in thickness. I am informed that the coral discourages these devils from molesting the graves.

Genus VARANUS Merrem

Monitor Lichtenstein, Zool. Mus. Univ. Berlin, ed. 2, 1818, p. 66 (*non* Blainville 1816).

Varanus Merrem, Tentamen systematis amphibiorum. Marburg, 1820, p. 58 (type of genus, *Lacerta varia* Shaw).

Diagnosis: Very large lizards, reaching 1 to 3 m. in length; head covered with small juxtaposed scales, body with even smaller scales and, except in very young specimens, each scale surrounded by a rosette of tiny granular scales; tongue very long, slender, deeply bifid, retractile into a sheath; ventrals quadrangular, arranged transversely; a single pair of preanal pores present, their openings just in front of vent; small pits present on scales, those before vent and on thighs somewhat different from others. Osteoderms present. Tail elongate, not fragile; pupil round; eyelid well developed. Five species are represented in Thailand.

KEY TO THAI SPECIES OF VARANUS

1. Enlarged scales on dorsal surface of neck rather widely spaced; nostril oblique, twice as far from end of snout as from orbit 2
   Scales on neck not widely spaced nor especially enlarged; distance of nostril from tip of snout variable, but nearer to end of snout than to orbit 3

2. Enlarged flat neck-scales arranged in 10-12 longitudinal rows, the posterior ones keeled; dorsal scales strongly keeled. Blackish above, neck and anterior part of body yellowish with three black longitudinal stripes on head and neck; two black bands across shoulders, *rudicollis*

Enlarged flat neck-scales not arranged in distinct rows; dorsal scales slightly enlarged, strongly keeled; snout depressed at end; head light brown to yellowish-brown with a pair of black streaks from eye joining a transverse dark band on neck; back with four rather distinct broad darker bands narrowly separated by light dotted bands, except one on neck wider and more distinct . . . . *dumerilii dumerilii*

3. Snout depressed at end, half as long as head; nostril rounded or oval, twice as far from orbit as from tip of snout. Thai specimens usually with five or six transverse bands of yellow ocellated spots across back; head banded anteriorly with black, ventrals keeled, *salvator salvator*

Snout not depressed at end; nostril not twice as far from orbit as from end of snout; ventral scales smooth 4

4. Nostril a little nearer to end of snout than to orbit; supraocular scales only slightly enlarged; olive or yellowish brown above with irregular darker markings which may form dark crossbars; a blackish temporal streak, below yellow with more or less distinct crossbars, *flavescens*

Nostril much nearer end of snout than to orbit; four or five transversely enlarged supraoculars; nuchal scales not keeled; other scales keeled on body; olive-black on body with numerous small yellow spots not forming well-defined crossbars; a dark temporal stripe from eye merging with dark marks on neck . . . . . *bengalensis nebulosus*

Varanus rudicollis (Gray)

FIG. 57

Uaranus rudicollis Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 10 (type-locality, Philippine Islands).

Varanus rudicollis: Boulenger, Catalogue of the lizards in the British Museum, 2nd Ed., vol. 2, 1885, p. 313 (Sarawak, Borneo); Flower, Proc. Zool. Soc. London, 1896, p. 873 (Malay Peninsula); *ibid.*, 1899, p. 643; Hanitsch, Checklist of the reptiles and amphibians in Raffles Museum, 1901, p. 2; Laidlaw, Proc. Zool. Soc. London, 1901, p. 310 (Perak); Boulenger, Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 174; Barbour, Mem. Mus. Comp. Zool., vol. 44, p. 183; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 78 (Trang, first report from Thailand); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, No. 1, 1916, p. 55 (Trang, Thailand); Chasen and Smedley, Journ. Mal. British Asiat. Soc., vol. 5, p. 352.

V[*aranus*] (*Dendrovaranus*) *rudicollis:* Mertens, Abh. Senckenb. Naturf. Gesel. Abh. 462, 465, 466 (all continuous pagination), 1942 pp. 195, 360-363, pl. 12, fig. 56, 57, pl. 13, fig. 65, pl. 15, fig. 94; Senckenbergiana biologica, vol. 40, No. 5/6, 1959, p. 224.

Varanus scutigerulus Barbour, Proc. New England Zool. Club, vol. 13, p. 1 (type-locality, Kampong Ulu, Sarawak N. Borneo).

Varanus (*Varanus*) *salvator scutigerulus:* Mertens, Senckenbergiana biol., vol. 40, No. 5 & 6, 1959, p. 259.

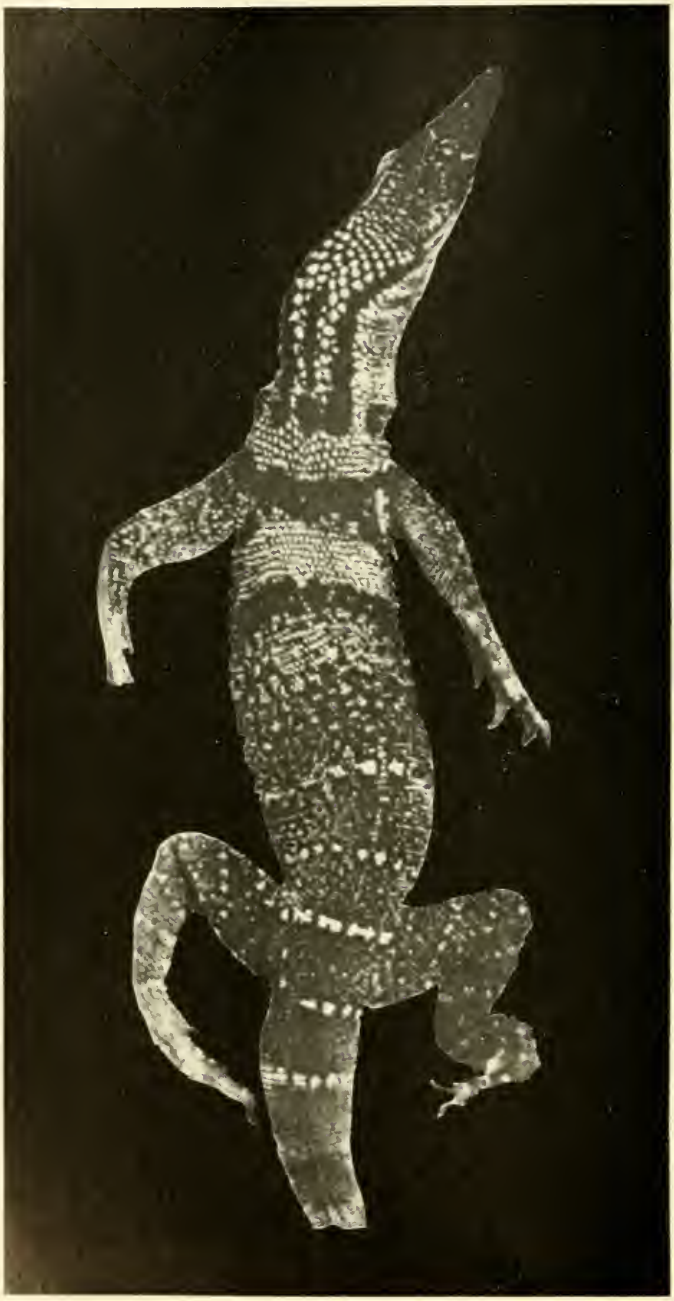


FIG. 57.—*Varanus rudicollis* (Gray). From Mertens, Abh, senckenb. naturf. p. 98, pl. 12, Ges., 462, 1942, p. 98. Tafel 12, fig. 56.

Diagnosis: Nostril oblique, distance between eye and nostril half that between nostril and tip of snout; three to six transversely widened supraocular scales; large prominent scales on nuchal region, strongly keeled, forming ten to twelve longitudinal series; ventral scales keeled; body with yellow transverse bands or rows of ocelli; sides of neck yellow (reddish in life).

Description of species (from No. 666 near Ranong, Ranong province, Thailand): Snout rather pointed, elongated, somewhat less than half length of head; nostril one half as far from eye as from tip of snout; distance between eye and ear (15 mm.), greater than distance between eye and nostril; canthus rostralis distinct; a longitudinal depression or groove on snout and a groove on lower jaw; rostral small, followed by two scales; a series of transversely widened supraoculars, anterior ones smallest; scales in temporal region very small; tympanum large, superficial, the posterior part concealed by a slight skinfold; a small fold from jaw angle to shoulder more or less continuous with a slight fold from shoulder to groin.

Scales on neck compressed forming high keels, arranged in ten or twelve series gradually merging into the smaller lateral nuchal series; scales on limbs and dorsum small, somewhat larger on back than on sides and flanks; ventrals strongly keeled; tail compressed with a double-keeled low median crest; scales on tail arranged in nearly regular transverse series, equal-sized proximally, the ventral subcaudals becoming larger distally; a pair of preanal pores in male, widely separated.

Eye-opening nearly of same size as tympanum; teeth compressed, pointed.

Color: Top of head generally brownish or olive-brown, most scales having a darker center; scales on snout a little larger than those in frontal and occipital regions; a pair of black stripes begin behind eyes, that extend back as far as a black transverse band in front of shoulders; area between bands on dorsal surface brownish; sides of neck, below longitudinal stripes, and underside, yellowish (reddish in life), with some black areas on sides of throat and under chin; an irregular yellowish bar across shoulders followed by a black irregular bar with extensions onto arms; this followed by a broad yellow band reaching to slight lateral fold; across middle of back a double row of ocelli preceded and followed by indefinite dark bands; next follows a row of single ocelli; a faint yellowish band between hind legs; arms and legs with some yellow spots; a distinct yellow spot at base of each claw dorsally; venter with in-

definite yellowish bars separated by a darker area. Tail generally olive-brown, with two basal bands discernible; yellowish in subcaudal region.

Measurements in mm.: Snout to vent, 306; tail, 426; total, 732; snout to arm-insertion, 140; axilla to groin, 114; head length, 68; head width, 26.5; arm, 103; leg, 160. (From a mounted specimen in Chulalongkorn; the measurements are not accurate but close approximations).

Distribution: The species is known from the provinces of Ranong and Trang, in Thailand. It doubtless occurs in other southern peninsular provinces but is regarded as a rare species.

Outside of Thailand the species occurs in Southern Burma, Malaya, and islands of Sumatra, Borneo, Banka, reaching as far as the Philippines. There is a doubtful record for Celebes.

Remarks: The description is drawn from a mounted specimen. It was taken near Ranong in the province of the same name. It is perhaps the most northern locality record of this species; Boulenger (1912) has reported its presence in Trang province previously.

The species is conspicuous in having the large nuchal scales with high compressed keels, arranged more or less in series, and cannot be mistaken for another species.

Boulenger's 1912 description of the color markings differs somewhat: "Blackish above, the neck and anterior part of the body yellowish, the former with three black longitudinal streaks, the latter with two broad transverse black bands; hinder part of back and flanks with yellowish ocelli; limbs with yellowish spots; lower parts with black reticulations." It is said to be a jungle form.

Varanus dumerilii (Schlegel)

Monitor dumerilii Schlegel, Abbildungen amphibiorum, 1839, p. 78 (type-locality Bandjermasin, S. Borneo).

Two subspecies are recognized. The typical form only is known from peninsular Thailand.

Varanus dumerilii dumerilii (Schlegel)

Monitor dumerilii Schlegel, Abbildungen neuer oder unvolständing bekannter Amphibien . . . 1839, p. 78 (type-locality, Bandjermasin, Borneo); Günther, Proc. Zool. Soc. London, 1872, p. 588.

Varanus macrolepis Blanford, Journ. Asiat. Soc. Bengal, vol. 50, pt. 2, p. 239, pl. 16 (type-locality, Tenasserim, Burma).

Empagusia flavescens: Blyth, Proc. Asiat. Soc. Bengal, vol. 22, p. 412 (Mergui).

Varanus dumerilii Bleeker, Nat. Tijdschr. Ned. Ind., vol. 16, 1858, p. 188 (Borneo); Boulenger, Catalogue of the lizards in the British Museum, vol. 2, 1885, p. 312; The fauna of British India . . . Reptilia and Batrachia,

1890, p. 165; Proc. Zool. Soc. London, 1890, p. 33; Werner, Verh. Zool. bot. Ges. Wien., vol. 46, p. 12; Annandale, Journ. Asiat. Soc. Bengal, new ser., vol. 1, 1905, p. 90; Barbour, Mem. Mus. Comp. Zool., 1912, vol. 44, p. 183 (Burma, Borneo, Sumatra); Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 77-78; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 54; Journ. Federated Malay States Mus., vol. 10, 1922, p. 269 (Pahang, Malaya); The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 405-406.

V[aranus] (Tectovaranus) dumerilii dumerilii: Mertens, Abh. Senckenb. Naturf. Ges., Abh. 462, 465, 466, 1942, pp. 263-264, pl. 11, fig. 63; pl. 17, fig. 117; pl. 22, figs. 150, 151; pl. 27, fig. 211; pl. 31, fig. 248, 249; pl. 32, fig. 264; pl. 34, fig. 292.

Diagnosis: Nostril an oblique slit, twice as near orbit as to end of snout; scales in nuchal region two to three times size of scales on top of head; canthus rostralis distinct; tail compressed with a double-toothed crest. Two black dorsolateral head-bands join a black band about neck, the ring followed by a narrower cream-band. Body blackish or dark brown with three narrow dotted or continuous cream-bands.

Description of species (from half-grown specimen Khao Chong, Trang *):

Snout somewhat convex, depressed at tip, its length two and one-half to three times its height; nostril situated twice as close to eye as to tip of snout; distance between ear and orbit greater than distance between eye and nostril; posterior edge of tympanum less superficial than front edge; rostral small; 15 supralabials followed by five scales bordered internally by small concealed granules; 18 infralabials followed by five scales bordered internally with granules; mental small its labial border not or scarcely larger than that of rostral, bordered behind by two scales that are the first of two scale series separated by a groove. Rostral followed by two scales, and these by three scales all larger than surrounding scales; five scalerows of unequal size in interocular region; five unequal rows above each eye, the scales not conspicuously widened; occipital scales about equal to those of frontal area; none of head scales keeled, anterior ones with numerous "pits."

Dorsal scales on neck two to three times size of head scales all strongly but bluntly keeled (except a few anteriorly) the enlarged scales extending back nearly to level of arm-insertion; scales on dorsum rather large but smaller than those in nuchal region, varying a little in size, all rather sharply keeled, smallest scales occurring low on sides, all arranged in more or less distinct transverse rows; ventral scales smaller than lateral body scales, arranged in about 65 transverse rows from axilla to groin; smooth scales on exposed

* Specimen from Forestry Department, collected by Nai Dumrong Chaiglom, later presented to Chulalongkorn University.

parts of limbs; tail strongly compressed, the keeled scales arranged in transverse rows or whorls; upper scales on tail in two denticulate rows highest at base of tail; lateral caudal scales smaller than ventral caudal scales. Limbs pentadactyl third and fourth fingers equal; rows of flat scales under digits; fourth toe longest, with 17 transverse rows of scales on under surface.

Color: Brownish to brownish black with five more or less regular cream to yellow transverse bands, first widest, between or slightly in advance of arms, fifth between legs; throat and neck yellowish. A pair of dorsolateral blackish stripes on head that join a blackish transverse nuchal band. Arms and legs with yellow spots and flecks; yellow band preceding groin, somewhat ocellate; base of tail with indefinite yellow bands, indistinct or absent distally; venter banded with black bands and rows of ocellated yellow spots.

Measurements in mm. (from M. Smith, 1935): Snout to vent, 500; tail, 750; total, 1250 (largest specimen).

Variation: The young are nearly black or brownish black and markings are very distinct. The upper side of the head is bright yellow (perhaps reddish in life). Mertens 1942 has separated *d. dumerilii* from *d. heteropholes* on the character of the scales. In the former scales at base of the tail on neck and back are more or less similar; in the latter the scales on tail vary between small and large, while scales on neck and back are distinctly dissimilar.

Distribution: In Thailand the species has been taken in Trang province near the Forest Experimental Station at Khao Chong.

It is known outside of Thailand in Tenasserim, Malaya, Sumatra, Borneo, and a few smaller islands.

Varanus salvator (Laurenti)

Stellio salvator Laurenti, Specimen medicum exhibens synopsin reptilium emendatam (type locality "America" *ex errore*).

Several subspecies of this widely distributed species are recognized, only one of which, the typical one, occurs in Thailand.

Varanus salvator salvator (Laurenti)

FIG. 58

Stellio salvator Laurenti, Specimen medicum, exhibens synopsin reptilium emendatam . . . 1786, p. 56 (based on Seba, Thesaurus, vol. 2, pl. 88, fig. 2 type locality, America *ex errore*).

Varanus salvator: Cantor, Journ. Asiat. Soc. Bengal, vol. 16, pt. 2, 1847, p. 635, published separately as, Catalogue of reptiles inhabiting the Malayan peninsula and Islands, collected or observed by Theodore Cantor, Esq., M. D., p. 29; Boulenger, Catalogue of the lizards in the British Museum (Natural History) Ed. 2, vol. 2, 1885, p. 314; The fauna of British India . . .

Reptilia and Batrachia, 1890, p. 166; Laidlaw, Proc. Zool. Soc. London, 1901, p. 309; M. Smith, *ibid.*, vol. 2, pt. 2, Dec. 1916, p. 158 (Nakhon Si Thammarat and Pattani); Journ. Bombay Nat. Hist. Soc., vol. 35, 1932, p. 616; Journ. Nat. Hist. Soc. Siam, vol. 2, pt. 1, June 1916, p. 55 ("Common about Bangkok"); Flower, Proc. Zool. Soc. London, 1896, p. 873, Boulenger, Fasciculi Malayenses, vol. 1, Zoology, 1903, p. 187.

Varanus salvator salvator: Mertens, Senckenb. Naturf. Ges., Abh. no. 466, 1942, pp. 245-253; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1042, 1101.

Diagnosis: A large species reaching in excess of two and one-half meters in length; snout long, three times as long as high, nostrils round or oval, twice as far from orbit as from tip of snout; median supraoculars enlarged. Scales on crown of head larger than nuchal scales; dorsals scales keeled; ventrals feebly keeled; young blackish with transverse rows of rather large yellow ocelli. Below yellow; tail banded black and yellow throughout.

Description of species (from No. C.860 from "near Bangkok"): Head elongate, snout more than half total length; nostril an elongate oval its distance from tip of snout half distance to orbit; rostral small, not wider than adjoining supralabials of which there are about 36 to mouth-angle, last five or six may be somewhat irregular; a groove from below nostril to eye, separated from lip for most of its distance by four scalerows (including infralabials); a longitudinal depression between and back of nostrils; a constriction of snout somewhat behind nostrils; seven or eight transversely widened supraoculars; median frontal scales nearly as large as largest nuchal scales; all scales on head smooth each with two or more pits; scales equal in temporal regions and area posterior to tympanum, smaller than other head scales; tympanum superficial, about as large as eye-opening, its posterior border partly covered by a skin-fold; mental no larger than adjoining infralabials, followed by two scales the first of two scale series separated by a longitudinal groove; a rather indistinct nuchal fold; dorsal scales keeled with an "apical" pit; distal subcaudal scales enlarged and strongly keeled; tail compressed, triangular in cross section; a double-toothed crest on top of tail; lateral scales forming small subequal transverse rows, growing larger at base and merging with larger subcaudal scales; pits on most lateral scales strongly developed.

Limbs strong, pentadactyl, clawed; digits surrounded by transverse rows of small scales, median series not modified; fourth toe longest with about 32 rows, scales of inner edge larger, tubercular; terminal scale above on digits enlarged, yellow; venter with transverse rows of subequal scales, about 80 between axilla and groin.

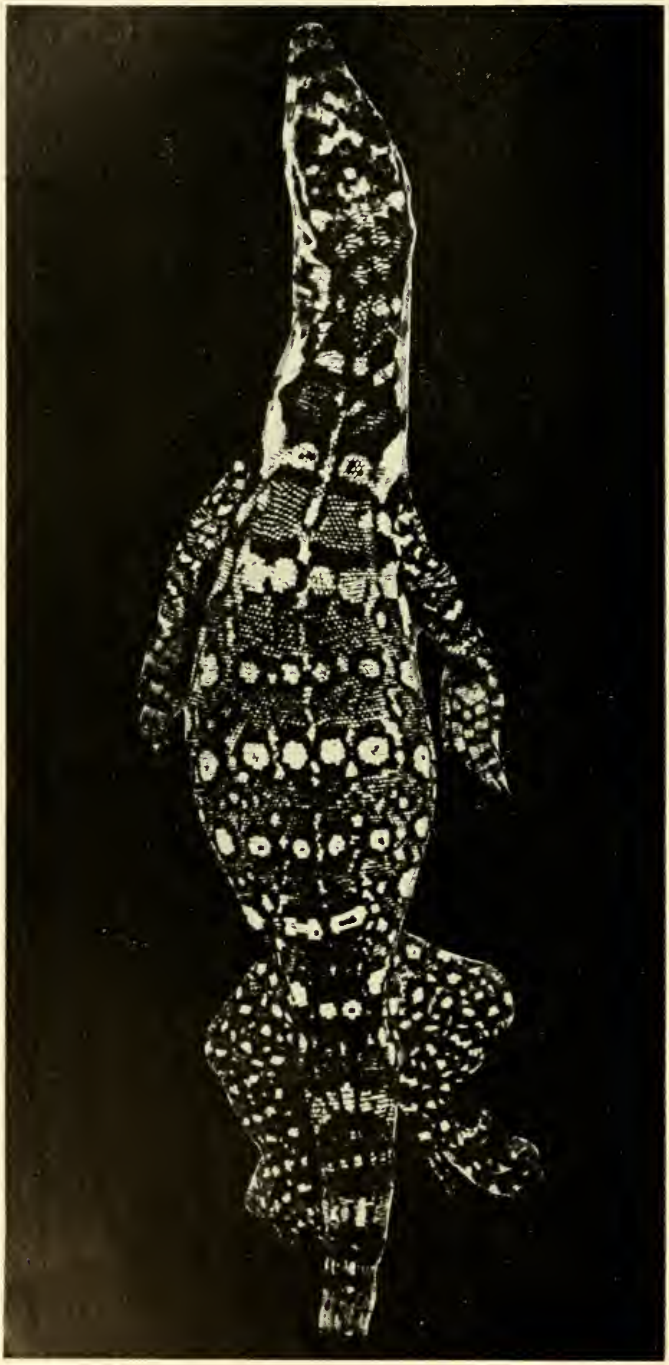


FIG. 58.—*Varanus salvator salvator* (Laurenti). From Mertens, Abh. senckenberg. naturf. Ges., 462, 1942, Tafel, fig. 21.

Two preanal pores on right side, one on left. A lateral fold indicated; pineal eye rather large, yellow in color.

Osteoderms present.

Color: Above olive-brown on top of head, largely yellowish to amber on sides of head; two yellowish spots above and around nostrils and one covering tip of snout; neck brown mixed with yellowish, the yellow growing more evident on sides of neck while undersurface is all yellow save for a few black flecks and spots suggesting incomplete transverse bars; arms and legs brown, punctate with yellow spots, the size of one scale, or larger on leg; back traversed by five rows of ocelli (black surrounded by yellow); tail banded but darker bands largely infiltrated with yellow and yellow bands with brown. Distally brown bands nearly uniform, the yellow bands, however, have longitudinal streaks; subcaudal region uniform yellowish.

Measurements in mm.: Snout to vent, 433; tail, 716; total length, 1149; snout to arm-insertion, 177; axilla to groin, 170; head width, 45; head length, 80; arm, 137; leg, 180.

Distribution: This subspecies has a wide distribution from India and Ceylon east and south through southeastern Asia, the Malay Peninsula and Indo-Australian Archipelago to the Philippines, Celebes, and northern Australia.

Remarks: This genus has been monographed by Dr. Robert Mertens in the Abhandlungen der Senckenbergischen Naturforschenden Gesellachaft Abhs. 462, 465, and 466. A remarkable literature list and bibliography of this species contains more than 250 items.

In size, this species is second only to the "Komodo Dragon." Specimens measuring 2500 meters have been reported and they may even reach a larger size. It is probably the most widely distributed species of *Varanus*.

The young specimens have the markings clearly defined but these fade as the animal grows older and in many of the larger animals the pattern is almost completely lost, the color becoming dark olive with indistinct yellowish markings. In Thailand the species occurs throughout the country in suitable localities. They haunt the banks of streams and klongs and the seacoast in the vicinity of rivers.

Eggs are placed in hollow trees or where these are not available in holes near water.

The species is at least chiefly carnivorous and often feeds on meat in a rather advanced state of decay. Occasionally (in the southern part of the Philippines), they disinter corpses buried in shallow graves.

Varanus flavescens (Hardwicke and Gray)

Monitor flavescens Hardwicke and Gray, Zool. Journ., vol. 3, p. 226 (type locality, India).

Empagusia flavescens: Gray, Ann. Nag. Nat. Hist., vol. 1, 1838, p. 393 (India); Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 9; Günther, Proc. Zool. Soc. London, 1860, p. 159; *ibid.*, 1861, p. 215.

Varanus flavescens: Cantor, Journ. Asiatic Soc. Bengal, vol. 16, 1847, p. 634 (Penang, Bengal, Nepal); Günther, The reptiles of British India, 1864, p. 65, pl. 9, fig. A; Theobald, Journ. Linn. Soc., vol. 10, Zool., 1868, pp. 23, 35; Theobald, in Mason, Burma, its people and productions, vol. 1, 1882, p. 326; Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Cambodge, 1885, p. 76; Boulenger, The fauna of British India . . . Reptilia and Batrachia, 1890, p. 164; Boettger, Katalogue of the reptilien Sammlung . . ., 1893, vol. 1, p. 70; Boulenger, Fasciculi Malayenses, Zool., vol. 1, 1903, p. 174 (Malaya); A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 76 (Nepal, Bengal, Burma, Malay Peninsula [Trang and Penang]); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916; Journ. Bombay Nat. Hist. Soc., vol. 35, 1932, p. 616; The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 404-405; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 30, 1958, p. 1101 (in list).

Varanus (Empagusia) flavescens: Mertens, Abh. Senckenb. Naturf. Ges., Frankfurt am Main, Abh. 462, 465, 466, 1942, pp. 187-189 and 347-349, pl. 1, fig. 4, pl. 16, fig. 110 (the pagination continuous in the three numbers).

Diagnosis: A small species reaching about one meter in length with a short broad head; nostril slitlike nearer to tip of snout than to eye; median supraorbital scales widened transversely. Other head scales subequal; ventral scales smooth.

Description of species (from literature): Head rather short broad, snout convex rather than depressed or flattened; nostril elongate, oblique, slitlike, nearer end of snout than to orbit; distance from eye to ear-opening a little greater than distance between eye and nostril; about 18 supralabials and a similar number of infralabials; teeth subconical scarcely compressed. Dorsal head scales subequal save those in supraocular region somewhat widened transversely, nuchal scales larger than head scales, all of which are keeled; scales on venter in 65-75 transverse rows; limbs moderate, digits rather shorter proportionally than in other species. Tail strongly compressed with a double-toothed crest above subcaudal scales slightly larger than lateral scales which tend to form somewhat irregular transverse rows.

Color: Greenish or brownish olive, with irregular indistinct darker markings which usually become confluent to form cross-bars on back and tail; throat with dark irregular transverse bands.

Measurements in mm. (from M. Smith, 1935): Snout to vent, 365; tail, 465.

Variation: Mertens states that the head scales are rather large and smooth while the neck scales are larger than the posterior head scales and smooth or keeled. In the young the markings are strongly defined. Above they are dark brown with yellow flecks. A dark temporal stripe is present.

Distribution: The species in Thailand is known only from the Boulenger report from Trang (province). Elsewhere it has a wide distribution in northern India from the Punjab to western Bengal, and south through Burma to Malaya (Penang) and Indo-China.

Remarks: This is the smallest species of the genus to occur in Thailand. Those known are less than a meter in length.

Theobald, 1868, states (p. 23): "Large specimens are not often procurable as they are much sought after by both Birmese and Karens as choice articles of food. They are hunted chiefly with dogs, whose scent enables them to discover the large Varans in the hollow trees in which they habitually shelter themselves.

"The Varani deposit their eggs in the ground usually selecting a deserted white ants' nest. The eggs are cylindrical, with tapering ends, of a dirty-white color and leathery texture . . . they are oily and feculent-looking, though devoid of any nauseous odor; and some Europeans eat them with pleasure."

Varanus bengalensis (Daudin)

Tupinambis bengalensis Daudin, Histoire naturelle des reptiles, vol. 3, 1802 (An XI), p. 67 (type-locality, Bengal).

Two subspecies are recognized, the typical one from India, and *nebulosus* with a range from southern Burma, Thailand, and Annam, throughout Malaya and Java. It is remarkable that it is unknown in Sumatra (*fide* Mertens).

Varanus bengalensis nebulosus (Gray)

FIG. 59

Monitor nebulosus Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9, 1831, Synopsis, p. 27 (type-locality, Java).

Varanus nebulosus: Cantor, Journ. Asiat. Soc. Bengal, vol. 16, 1847, p. 633; Günther, The reptiles of British India, 1864, p. 66, pl. 9; Boulenger, Catalogue of the lizards in the British Museum, vol. 1885, p. 331; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 165; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 77; Fasciculi Malayenses, vol. 1, Zoology, 1903, p. 157; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, pt. 1, 1916, p. 54; *ibid.*, vol. 2, pt. 2, Dec. 1916, p. 155 (Patani, Nakhon Si Thammarat and Prachuap Khiri Kan); H. C. Smith, Journ. Bombay Nat. Hist. Soc., vol. 34, 1930, p. 370; Theobald, Journ. Linn. Soc., vol. 10, Zoology, 1868, p. 22; M. Smith, The Fauna of British India including Ceylon and Burma, . . . Reptilia and Amphibia, 1935, pp. 403-404.

Monitor nebulatus: Schlegel, Abbild, Amphib., 1839, p. 75.

Varanus bengalensis nebulosus: Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1042, 1101-1102.

Varanus (Indovaranus) bengalensis nebulosus: Mertens, Abh. Senckenb. Naturf. Ges., Abh. no. 466, 1942, pp. 244-252, pl. 11, fig. 15.

Diagnosis: Scales on neck not strongly enlarged; nostril elongate, twice as close to the eye as to tip of snout; a series of five or six widened supraocular scales. Scales on dorsal surface suggest half covered eggs, each with a well-defined apical pit; they may be somewhat keeled; scales on neck only slightly larger; subcircular without keels. Dark above without transverse bands; two chevron-shaped dark marks on neck, anterior reaching to eyes; two broad dark bands on tail separated by smaller cream bands on distal part of tail; digits clawed, compressed, third and fourth fingers of equal length with about twenty transverse rows of scales surrounding digit; fourth toe longest, with about 25-28 transverse rows of scales. A row on inner basal region enlarged. Ear larger than eye-opening, posterior surface of tympanum partly covered by a fold of skin.

Description of species: Snout long, approximately equal to half length of head; nostril only slightly closer to eye than to tip of snout *; rostral small followed directly by paired scales, the first of two series forming a longitudinal groove on snout; 21 supralabials followed by five or six smaller scales to rictus oris; scales in frontal area larger than elsewhere on top of head. Four or five widened scales in supraocular region. All head scales with numerous "pits"; infralabials about 25, followed by a few smaller scales to rictus oris; mental scarcely larger than rostral, followed by two scales which are first of two enlarged regular rows, separated by a deep groove.

Scales on neck flattened, somewhat rounded or oval, not keeled, each with a pit; dorsal scales smaller, keeled, all in more or less straight transverse rows; ventral scales in about 70 transverse rows between axilla and groin, flat, rounded posteriorly; a pair of small preanal pores; a strong nuchal fold. An indistinct lateral nuchal fold; lateral fold on body scarcely indicated; tail triangular in cross-section with a double-toothed crest above, the scales on side of tail in transverse (vertical) rows; those on ventral surface of tail somewhat larger.

Color: Above blackish with numerous yellow scales scattered over arms, legs, on dorsum and sides. On the back the larger dots

* Boulenger (1912) description says, "nostril elongate, oblique, nearly twice as distant from end of snout as from orbit." This is probably in error. The same relationship is also indicated in the key.

FIG. 59.—*Varanus bengalensis nebulosus* (Gray). Young specimen, Pattani, Pattain province, *circa*. Natural size.

of yellow are usually surrounded by black scales forming small ocelli that are arranged in rather indefinite rows across back and base of tail. Chin with transverse bars of yellowish white and black; neck marbled. Underside of limbs with rosettelike groups of whitish scales; venter mottled white or yellow, and slate. Tail variegated and streaked except for two broad bands of black separated by narrower ones of yellow. Fingers with a yellow dorsal line and all digits with a yellow spot at base.

Measurements in mm.: Snout to vent, 220; tail, 348; width of head, 26; length of head, 52; arm, 74; leg, 96.

Remarks: Younger specimens are olive to black (snout to vent, 140 mm.), and have the chin strongly barred in bluish and yellow-cream; bars chevron-shaped, white on neck, very irregular; on breast and venter about 15 dark transverse bands with very irregular edges separated by rows of whitish spots more or less confluent; rounded or rosette light spots under limbs; head blackish with a series of white spots on upper lip; neck with a pair of dim dark lines from eyes meeting on neck; another chevron-shaped mark following it; back with numerous (16-17) transverse rows of tiny ocelli; arm and leg with punctate spots much smaller than on underside; two cream bands distally on tail; and two broader black bands.

Distribution: This species is very wide-spread in Thailand being known from Malaya north to Chiang Mai province, and east to Laos and Cambodia.

Outside of Thailand it is in Burma, Viet Nam, and Malaya. All specimens I have collected were found in trees.

The figure given is of still another young specimen.

FAMILY LACERTIDAE Cope

Lacertinidae, Gray, Ann. Philos., vol. 26, 1825, p. 200.
Lacertidae Cope, Proc. Acad. Nat. Sci. Philadelphia, 1864, p. 228 (*part.*).

Top of head covered with symmetrical shields. Tongue deeply notched and covered with scalelike papillae, or plicae; four limbs, well developed. Femoral pores present.

A single premaxillary bone; both nasal and frontal bones paired, parietal single; postorbital and frontosquamosal arches present; dermal bones on head and above fossae, none on body; dentition pleurodont.

This family is confined to the eastern hemisphere with a single genus entering Thailand.

Genus TAKYDROMUS Daudin

Takydromus Daudin, Histoire naturelle des reptiles, vol. 3, 1802, p. 251 (type of genus, *quadrilineatus*).

Tachydromus Günther (emendation), Ann. Mag. Nat. Hist., series 6, vol. 1, 1888, p. 166.

Head shields consisting of rostral, frontonasal, prefrontals, a frontal, supraoculars, frontoparietal, interparietal, parietals, and occipital; nostril between three scales; lower eyelid scaly; dorsal surface of body with enlarged series of keeled shields that form continuous ridges; several series of fine granular scales along side.

Ventrals large, keeled, in definite rows. Limbs well developed. One to three femoral pores on each side.

Some 12 forms are recognized that range from China and Japan to Indo-China, Thailand, Burma, India, and northern Malaya.

Takydromus sexlineatus Daudin

In Thailand only a single species is known. Only one of its two subspecies has been found within the country the other is likely to occur.

KEY TO THE SUBSPECIES OF TAKYDROMUS SEXLINEATUS

Two preanal pores on each side; head-shields smooth except frontal, which is keeled ..... *s. sexlineatus*

One preanal pore on each side; head-shields rugose or keeled ..... *s. ocellatus*

Takydromus sexlineatus ocellatus Cuvier

FIG. 60

Takydromus ocellatus Cuvier, Guerin, Icon. Règne Animal., Reptilia, 1829, pl. 5, fig. 3 (type-locality, "les Indes orientales"); Duvernoy, Règne Animal., Reptilia, 1836, pl. 11 (Cochin-China regarded as probable type-locality).

Tachydromus typus Gray, Ann. Mag. Nat. Hist., vol. 1, 1838, p. 389 (type-locality, China).

Tachydromus typicus Gray, Catalogue of the lizards in the collection of the British Museum, 1845, p. 52.

Tachydromus meridionalis Günther, The reptiles of British India, 1864, p. 70, pl. 8, fig. D (type-locality, S. China).

Tachydromus sexlineatus meridionalis: Stejneger, Proc. U. S. Nat. Mus., vol. 66, 1925, p. 55; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, pp. 419, 487.

Tachydromus sexlineatus: M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 155; *ibid.*, vol. 6, 1923, p. 200; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 79.

Takydromus sexlineatus: M. Smith, Bull. Raffles Mus., no. 3, 1930, p. 29.

Tachydromus sexlineatus ocellatus: M. Smith, The fauna of British India . . . Reptiles and Amphibia, vol. 2, Sauria, 1935, pp. 368-369.

Diagnosis: A tail nearly four times as long as distance from snout to vent; six enlarged scalerows on neck and front half of body followed by four, all strongly keeled, keels forming continuous lines;

nasals meeting on median line; frontal with a ridge or keel; 10-14 ventral rows of enlarged keeled scales, keels forming continuous straight lines; a single preanal pore on each side. Anal scale single, large flanked by two small scales on each side.

Description of species (from No. 35520 from near Rompibon, Tonka Harbour Tin Mine), Nakhon Si Thammarat): Rostral large, suture between rostral and first labial directly below nostril; nasals in broad contact behind rostral; frontonasal longer than broad touching one loreal; prefrontals elongate, broadly in contact; frontal with a strong median keel; frontoparietals broadly in contact, larger than prefrontals; interparietal small; parietals with an irregular keel separated from each other by interparietal and a small "occipital" scale behind it; nostril between nasal, first supralabial and a postnasal; two loreals, second much the larger with an upper posterior process passing partly above first supraciliary; three supraoculars, first largest, last smallest; four (or three) supraciliaries; six supralabials, smooth except subocular (fifth) which is much elongated and with a strong curving keel; one presubocular; two or three postsuboculars; parietal bordered by three elongate keeled temporals, below which are about eight rows of smaller keeled temporal scales; a narrow elongate curved scale forms upper boundary of tympanum; latter rather deeply sunk, as large as eye-opening; mental very large, its labial border equal to that of rostral and two adjoining supralabials; three pairs of chinshields, first smallest in contact, second pair partly separated, third, much the largest, diverging, separated by from two to ten scales all bordering infralabials; five or six narrow infralabials; six mesial rows of enlarged keeled scutes on neck and shoulders; four rows at mid-body continuing to tail; scales on sides small; a large patch in groin and axillary region, while in the middle of body there are about five to seven rows of granules; twelve enlarged scalerows on venter, and ventrolaterally an outer row bordering these about half as large, all keeled, the keels forming straight lines as they do on dorsal scales; a mere suggestion of a collar; caudal scales strongly keeled, forming transverse rows, keels tending to form continuous lines.

Arms with large keeled scales except on underside of upper arm; fourth finger longer than third, nearly cylindrical with 17 lamellae below; leg with enlarged keeled scales except on underside and part of posterior surface of thigh; 23 lamellae on underside of fourth toe, basal ones divided. Eyelid scaled; 27 scales from collar to groin; anal a large single scale with two low keels indicated, flanked

by smaller elongate keeled scales; a specialized scale directly in front of single pore-scale on each side.

Color: Head dark-olive; body greenish olive growing lighter on sides; a narrow dark line begins on second loreal, passes eye and continues above tympanum to some distance on neck and shoulder;

FIG. 60.—*Takydromus sexlineatus ocellatus* Cuvier, in Guerin. No. 35520, Ronpibon, Nakhon Si Thammarat. Actual length, snout to vent, 55; tail, 208 mm.

on side of neck and temporal region ultramarine; sides bordered by a dim greenish white line that is bordered below by an indefinite light-olive line; venter bluish- to greenish-white, continued on subcaudal region; no indication of small ocellate spots on flanks.

Measurements in mm.: Snout to vent, 55; tail, 208; snout to arm insertion, 19.6; axilla to groin, 30; width of head, 6.6; length of head, 13.6; arm, 17; leg, 25.

Variation: On the neck of this subspecies there are six rows of large scales. In one specimen examined these did not pass beyond a line drawn between arms; in two others they reached approximately halfway between the arms and legs, where they reduce to four rows.

Usually in freshly caught or preserved specimens the ocelli are distinct in the males; however, these marks disappear after long preservation.

A recently preserved specimen from Mae Hong Son shows two or three ocelli present at the base of the tail. This specimen has a shorter fifth toe than other specimens and the underside of hand and foot and the lamellae under the digits are a very vivid lemon-yellow, the color sharply limited on heel and wrist as well as on the sides, foot, and hands. The base of the tail is noticeably swollen in males.

This specimen has the regenerated portion of tail measuring 74 mm., while the scales on the reproduced portion are smaller, the scales have almost the same characteristics as those of the original tail.

Distribution: This subspecies has been taken in Chiang Mai, Mae Hong Son, Bangkok, Nakhon Si Thammarat, and Pattani. It probably occurs throughout most of Thailand although nowhere does it seem to be common.

This form reaches Indo-China, South China, Hainan, and the northern states of Malaya and Burma.

Remarks: These long-tailed lizards are egg-layers, the clutch consisting of from two to four eggs.

The tail is extremely long, nearly cylindrical and not especially fragile.

The animal moves with considerable speed. They are said to run over the tops of long grass in search for food. I have not seen this.

Family Scincidae

This group of lizards was given family rank by John Edward Gray in 1825, and very little effort has been made to break it into other families except by Gray himself who in his Catalogue of 1845 proposed four other families for species which he had formerly placed in the family Scincidae. The four proposed families have not been recognized by taxonomists of the present century.

The family group may be defined as follows:

Skull covered over and united with a series of dermal bones also covering the supratemporal aperature; postfrontosquamosal arch complete in all except certain reduced burrowing forms.

Tongue, bifid in front, covered with imbricating papilla. Teeth pleurodont, usually conical, more rarely hooked or spheroidal; abdominal ribs or parasternae present in certain burrowing forms; scales covering body, limbs and tail; osteoderms present. Head likewise with osteoderms but outer surface covered with large symmetrical plates. Limbs variable, often absent; femoral and preanal pores absent; postanal pores may be present. Tail fragile, when broken off it is reproduced without vertebrae.

There is no general agreement in regard to the generic groupings in this family. There are about 650 species recognized, the smallest number being in the Western Hemisphere, where only four genera are represented. The areas most thickly inhabited by the skinks are South Asia, the Malayan Archipelago, the Philippines, and Australia.

The general habitat of the skinks is terrestrial but a considerable number of species of numerous genera have become arboreal or at least semiarboreal. However, in most cases, there has been no special modifications of the limbs or digits save for a freer movement of the digits and a strengthening of the claws.

A few species of *Emoia*, and *Leiolopisma* have the subdigital lamellae increased in number, permitting them seemingly to climb on smooth-leaved plants or smooth-surfaced trees.

One of the remarkable happenings in a number of genera of the Scincidae is that certain species seem to be losing parts of the limbs and the animals are preparing to assume a subterranean existence or they have already lost their limbs and have become somewhat snakelike in appearance.

In the Philippine genus *Brachymeles* one sees this process at its

best. This genus has some typical pentadactyl species, in which the length of limbs and of body is much as in the typical generalized lizard, the limbs touching or overlapping when adpressed. Another species has the limbs shortened, the body and tail lengthened; others in which varying numbers of the digits have been lost; others with all digits gone and only a stub of a limb present; others with all external trace of limbs gone.

The evolutionary happenings would appear to be following a specific trend. One might propose a formula for the results of mutations that bring about the changes. Thus starting with a typical pentadactyl species represented by 5-5, the following might represent the major stages of digit and limb loss:

STAGE	Digit condition	STAGE	Digit condition
1	5–5	8	1–2
2	4–5	9	1–1
3	4–4	10	0–1
4	3–4	11	0–0
4a	4–3	12	arm–leg
5	3–3	13	no arm–leg
6	2–3	13a	arm–no leg
7	2–2	14	no arm–no leg

One cannot assume that the digit is lost by a single mutation. It may require x-number of mutations to produce the total loss of a digit.

The fact that populations found at any of these major stages show but very little variation in the character and condition of the digits is, however, significant, and suggests that there may be at least a temporary fixation of the condition at these stages.

While the genus *Brachymeles* does not show all of the 14 or more possibilities, offered by the formula, a considerable number of these are present, each found with a continuous range and two or three may be found with their ranges overlapping. Despite these considerable, seemingly generic, differences between certain of these species, one is constrained to regard the group as belonging to a single genus because of basic similarities.

Since this ability to produce degradational forms appears in so many genera of the Scincidae one is likely to postulate that this type of behavior is an inherent possibility in any group of limbed lizards. However, in the case of the genus *Scelotes*, a curious mu-

tational behavior permits loss of digits on one side of the Mozambique channel, while on the other side on the African mainland, the limbs become reduced, the body elongates, but no digits are lost. Does this not suggest the presence of some inhibiting factor? or if not, that the mutation toward loss of digits is lethal on one side, and none survive in this condition?

In Thailand several genera seem to have been undergoing these degradational mutations and often the animal, only in the ultimate stages of the formula seems to have survived.

Examples of Asiatic lizards that seem to have survived because of having reached this degradational stage, are *Ophioscincus* with two species; *Barkudia* with a single species; *Ophisaurus* with two species; *Isopachus* with one.

Some other genera no longer have any known pentadactyl representatives: *Nessia* with species representing stages, 5, 7, 11, 12, (2) 13. *Dibamus* with several species, the females in stage 13, the males, stage 12.

Certain other genera are *Chalcidoceps*, stage 3, *Sepsophis*, usually stage 9, *Ophiomorus*, stage 5, and two forms with four fingers and three toes, stage 4a.

Lygosoma quadrupes and *Riopa haroldyoungi* represent pentadactyl species in which the body has elongated and the limbs have become small, but the five digits have been retained. Do these represent genera in which mutations involving digital loss are lethal?

The greater number of the degrational species show the hand keeping ahead of the foot in loss of digits. A few exceptions do occur as is indicated under *Ophiomorus*.

In Amphisbaena—another Order of reptiles, in one genus, *Bipes* (and the only genus with any trace of limbs) the arm has been retained with five, three, or two digits, while the leg is completely lost. One suspects that these forms may move into underground burrows backwards! Certainly *Bipes* that I have observed moves forward and backward in its burrows with nearly equal ease.

If one accepts the idea that mutations are miraculous—that is, happening by chance without any physical (internal or external) causation, one is being properly orthodox. On the other hand if one might be permitted to suspect that these mutations are stimulated (or caused), one might suspect that the relation of body to burrow might provide a mechanism that tends to trigger the mutation, were such possible.

KEY TO THE GENERA OF SCINCIDAE IN THAILAND

1. Palatine bones separated on median line of palate; nostril pierced in a single nasal, supranasals present; a paired frontoparietal, *Eumeces*
   Palatine bones meeting on mid-line of palate 2
2. Pterygoid bones separated; palatal notch extending forward to level of middle of eyes; supranasals present; legs pentadactyl, well developed ..... *Mabuya*
   Pterygoid bones usually meeting on palate, palatal notch not reaching level of centers of eyes 3
3. Limbs absent 4
   Limbs present 5
4. Frontonasal present; frontoparietals broadly in contact; no ear-opening; body slender, elongate, tail blunt or somewhat pointed at tip, *Ophioscincus*
   No frontonasal; frontoparietals separated; no ear-opening; body not slender; tail blunt ..... *Isopachus*
5. Supranasals present; tympanum deeply sunk 6
   Supranasals absent 7
6. Limbs elongate the leg reaching elbow when adpressed; lower eyelid scaly ..... *Dasia*
   Limbs usually short, the body often elongated; the lower eyelid scaly; adpressed limbs fail to meet ..... *Riopa*
7. Tympanum exposed, superficial; eyelid scaly; one, two, or three enlarged preanal scales ..... *Tropidophorus*
   Tympanum not superficial, but more or less deeply sunk 8
8. Lower eyelid with a transparent disc, frontoparietal double (rarely single) 9
   Lower eyelid scaled; limbs overlapping; frontoparietals double; rostral convex or flattened ..... *Sphenomorphus*
9. Ear-opening very distinct; frontoparietal single or double; nuchals present or absent ..... *Leiolopisma*
   Ear-opening hidden under scales; single frontoparietal; three of four pairs of nuchals; 18-20 scalerows about body; four black longitudinal stripes. Snout to vent, 38 mm. ..... *Saiphos*

Genus EUMECES Wiegmann

Lacerta (*part.*) Linnaeus, Systema naturae, 10th ed., vol. 1, 1758, p. 205.

Scincus (*part.*) Harlan, Journ. Acad. Nat. Sci. Philadelphia, vol. 4, pt. 2, 1824, p. 286.

Mabuya (*part.*) Fitzinger, Neue Klass. Rept., 1826, p. 23.

Euprepis (*part.*) Wagler, Nat. Syst. Amph., 1830, p. 161.

Eumeces Wiegmann, Herpetologia Mexicana, 1834, p. 36 (type, *Sincus pavimentatus*) (*part.*); Taylor, Univ. Kansas Sci. Bull., vol. 23, pp. 29-30, 1935.

Plestiodon Dumèril and Bibron, Erpétologie générale, vol. 5, 1839, p. 697 (subgenus); Gray, Catalogue of the species of lizards in the collection of the British Museum, 1845, p. 90 (genus).

Lamprosaurus, Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1852, p. 206 (type *Lamprosaurus guttilatus* = *Eumeces obsoletus*).

Eurylepis Blyth, Journ. Asiat. Soc. Bengal, vol. 23, p. 739 (type *Eurylepis taeniolatus*).

Mabuya Günther, Reptiles of British India, 1864, p. 82.

Platypholis (*non* Boulenger) Dugès La Naturaleza, 2nd ser., vol. 1, 1887, p. 486 (type, *Eumeces altamirani*).

Description: Maxillary and mandibular teeth conical or with rounded spheroid crowns variable in number; premaxillary teeth usually 7; pterygoid teeth present, variable in size and number; prevomerine teeth present or absent (usually two where present); palatine bones not meeting on median plane of palate, but varying in degree of proximity; pterygoids separated on median line.

Eyelids well developed, the upper variable; tympanum deeply sunk; nostril in a nasal, single, partly divided or more or less completely divided; supranasals present; four supraoculars; two prefrontals, two frontoparietals, parietals and a single interparietal. Limbs well developed, pentadactyl, clawed; digits subcylindrical or compressed, with transverse scales on undersurface which may be compressed, keeled, or padlike in character. Scales with osteoderms, more or less cycloid, imbricating, occasionally fusing dorsally into larger plates.

Only a single species is known to occur in Thailand. Elsewhere the genus has a distribution in Japan, China, Asia Minor, North Africa, North and Central America, and the islands of Bermuda.

Eumeces quadrilineatus (Blyth)

Fig. 61

Plestiodon quadrilineatus Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 652 (type-locality, China, presumably Hong Kong).

Eumeces quadrivirgatus Hallowell, Proc. Acad. Nat. Sci., Philadelphia, 1860, p. 502 (type-locality, Hong Kong).

Mabouia quadrilineata: Günther, The reptiles of British India, 1864, pp. 82-83, pl. 10, fig. E; Theobald, Journ. Asiat. Soc. Bengal, extra number, 146, 1866, p. 24 (Hong Kong).

Eumeces quadrilineatus: Bocourt, Mission Scientifique au Mexique et dans la Amérique Centrale, livr. 6, 1879, p. 423, pl. 22 D, fig. 5 (Cambodia); Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 381; Günther, Ann. Mus. Zool. St. Petersbourg, vol. 1, 1896, pp. 199-219 (Szechuan); Mocquard, La Review Coloniale, July, 1906 (1907), p. 37; Mell, Arch. Naturg., 88 abt. a, 10 Heft, 1922, p. 114; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, p. 428, fig. 12; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 8, no. 1, Dec. 1929, p. 49 ("Muak Lek near Korat," Siam); Taylor, Univ. Kansas Sci. Bull., vol. 23, 1935, pp. 452-457, pl. 40, fig. 1, text figs. 74-75; M. Smith, The fauna of British India, Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 339-340 (Doi Angka, Dong Paya Fai Mts., Siam).

Diagnosis: Two median dorsal scalerows broader than adjoining rows. A postnasal present; 20 to 22 scalerows around middle of body; a pair of dorsolateral greenish-white stripes from rostral to

some distance on tail; an outer lateral stripe beginning on lips, passes to groin and along the base of tail.

Description of species: Snout moderately short, portion of rostral visible above less than half size of frontonasal; supranasals large forming a median suture, touching postnasal and first loreal; frontonasal large, broader than long, touching anterior loreal; prefrontals forming a relatively broad median suture, and in contact with frontonasal, frontal, posterior loreal, first supraocular, first superciliary and anterior loreal, length of their common sutures in the order named; frontal relatively short, obtusely angulate at both ends, shorter than its distance from end of snout; frontoparietals elongate, larger than prefrontals or interparietal, forming a median suture; interparietal small, enclosed behind by large parietals; three pairs of nuchals, anterior pair shortest transversely.

Nasal moderate, divided; postnasal small but distinct, touching two labials; anterior loreal high and narrow, higher than posterior; latter longer than high; seven—eight supraciliaries, first larger than last; a small preocular, two postoculars; four supraoculars, three anterior touching frontal; two presuboculars and four postsuboculars; four enlarged scutes on lower eyelid, separated from subocular labial by three rows of granules; primary temporal square, touching triangular lower secondary temporal narrowly; upper secondary temporal large (broken into two parts on left side); tertiary temporal touches upper secondary but is separated from nuchal; seven supralabials (eight on left side), seventh very large, separated from ear-opening by two paired scales. Eighteen scales surround ear.

Mental large, with a labial border greater than that of rostral; six infralabials; two postmentals, second largest; three pairs of chinshields, posterior largest; anterior pair in contact.

Two median scalerows widest; 54 scales in a row from parietals to above vent; about 30 scalerows around occipital region at ear; 26 at constricted part of neck; 20 rows about middle of body. A well-developed wrist tubercle; 13 to 14 lamellae under longest fingers; 19 lamellae under longest toes; six preanals, the two median enlarged; subcaudal scales much widened; adpressed limbs overlap the length of seven scales; postfemoral scales not differentiated.

Color: Back dark gray-brown, head more yellowish brown, with a darker area in interparietal region. A silvery dorsolateral line from rostral extends along side to a point half way on tail, covering greater part of second scalerows but encroaching on median rows

FIG. 61—*Eumeces quadrilineatus* Blyth. No. 31791; 1780 m. Namlang (Mt.), Bankhok, Dan Sai, Loei province. Actual total length, 97 mm.

on base of tail; the light lateral line begins on lips and extends on fifth row to base of tail; lateral area between white lines colored like back; below on venter brownish cream.

Measurements in mm.: Snout to vent, 73; tail, 63 (regenerated; normal length probably about 125 mm.); snout to eye, 4.8; snout to ear, 14; snout to arm, 26; axilla to groin, 40; width of head, 12; arm, 22; leg, 28.

Distribution: The species has been taken only a few times in Thailand. The localities are, near Muak Lek (but in Nakhon Ratchisima province; Doi Nang Ka Mt., Chiang Mai province). I have a specimen (illustrated) taken in Loei Province, and a second specimen taken from the stomach of a *Natrix* from an uncertain locality.

Genus MABUYA Fitzinger

Mabuya, Fitzinger, Verzeichniss der im K. K. Zoologisch Museum zu Wien befindlichen In Neue Classification der Reptilien, 1826, pp. 23, 52 (type *Lacertus mabouya* de la Cèpede, *fide* Malcolm Smith, 1935, p. 257).

Diagnosis: Palatine bones in contact mesially, palatal notch entirely separating pterygoids, reaching forward to between eyes; pterygoid teeth present or absent; maxillary teeth conical or bicuspid; eyelids well developed, lower lid with a transparent disc or with a series of opaque scales; ear with tympanum deeply sunk; nostril in single nasal; supranasals present; prefrontals present; normally two frontoparietals (rarely united in a single shield); interparietal distinct or rarely united with parietals; limbs strong, well developed, pentadactyl. Digits with transverse lamellae inferiorly.

There are six species of this genus in Thailand, one species recognized with three subspecific forms. The following key will serve to distinguish the known forms of the country.

KEY TO THAI SPECIES OF MABUYA

1. Lower eyelid with transparent disc; 32-34 scalerows about body; dorsal scales with three strongly defined keels and six or more additional keels; no postnasal ..... *novemcarinata*
   Lower eyelid with several scales instead of a disc; postnasal present or absent 2
2. Scales finely striate, with two or three feeble keels; 26-30 scalerows around middle of body; tail very long; a postnasal ..... *longicaudata*
   Scales not striate; keeled 3
3. Five to seven dorsal greenish-white longitudinal lines or olive unicolor; 5-7 keels on dorsal and lateral scales; 24-28 scalerows around middle of body ..... *rugifera*
   Without five to seven greenish-white longitudinal lines; number of keels variable; not olive unicolor 4

4. Three to five keels on dorsal scales; 30-34 scalerows around body at middle; no specialized scales on leg forming "chigger refuge"; a postnasal present ..... *multifasciata*
Five, seven, or nine keels present at various points on body; a "chigger refuge" on lower leg; postnasal present or absent ..... *macularia*

In Malcolm Smith's treatment of this genus he referred to it (June 1916, p. 55) *Lygosoma praesigne* Boulenger. His comments on this follow: "The pterygoid bones being entirely separated, and the palatal notch extending forward as far as a line connecting the centres of the eyes, this species should be placed under *Mabuia* instead of under *Lygosoma* as hitherto, although its affinities, notably the absence of supranasals, are with the latter genus. The evidence for this transfer is based upon specimens obtained last year in the mountains of Nakon Sitamarat, and now lodged in the British Museum."

I do not regard this placement tenable. Should examination of the skulls of various species of *Mabuya* and *L. praesigne* prove the condition mentioned by Dr. Smith as constant then *praesigne* might well represent a monotypic genus. In practically if not all its external characters it is a member of the genus *Sphenomorphus*, lacking, as it does, the characteristic keeled scales, the enlarged second supraocular, the posteriorly truncate parietals; the paired supranasals, the several rows of granular scales between the supraciliaries and the palpebral scales, the characteristic auricular opening, small preanals, that are usually, if not always, characteristic of Southeastern Asiatic *Mabuya*.

Mabuya novemcarinata (Anderson)

FIG. 62

Euprepes novemcarinatus Anderson, Journ. Asiat. Soc. Bengal, vol. 40, 1871, p. 12 (type-locality, Mandalay, Burma).

Mabuia novemcarinata: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1888, p. 179; The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 187; A vertebrate fauna of Malaya from Singapore to the Isthmus of Kra . . . Reptilia and Batrachia, 1912, pp. 82-83; Flower, Proc. Zool. Soc. London, 1896, p. 873.

Mabuya novemcarinata: Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, p. 261; Bull. Raffles Mus., no. 3, Apr. 1930, p. 30.

Diagnosis: Supranasals usually in contact behind rostral; prefrontals usually separated or rarely touching; no postnasal; lower eyelid with an undivided transparent disc; dorsals and lateral scales with 7 to 11 sharp keels; 32 to 34 scales about middle of body.

Description of species (from No. 227, Coffee Camp near Na Bon, Nakhon Si Thammarat): Rostral broader than high, forming a

FIG. 62.—*Mabuya novemcarinata* (Anderson). No. 33751, Khao Chong, Trang province. Actual length, 145 mm.

broad angle above; pair of supranasals in contact mesially; frontonasal a little broader than long forming suture with frontal, and prefrontals, laterally touching anterior loreal; frontal longer than its distance from tip of snout, slightly longer than its distance from nuchal; two frontoparietals; interparietal as large as preceding scales, separating parietals, which are keeled posteriorly; a pair of nuchals each with about 15 keels; nostril in single nasal; no postnasal; two loreals, anterior as high but not as long as second; two presuboculars; prefrontals quadrangular, touching both loreals, first supraciliary and first two supraoculars; four supraoculars, second and third in contact with frontal; six supraciliaries, first and last largest; two or three postsuboculars; seven supralabials, fifth subocular, latter more than twice as wide as preceding supralabial; two anterior and three posterior temporals; mental with a labial border much larger than that of rostral; single postmental; first chinshields in contact, second pair separated by a scale; six infralabials; lower eyelid with large transparent disc; auricular opening with two well-developed anterior lobules. Dorsal and lateral scales strongly keeled, two keels much stronger than others; altogether they vary from seven to ten although nine is probably most frequent number; temporal scales at least partially keeled; scales on limbs with three to five keels; all ventral scales smooth; 34 scalerows around middle of body; six to eight preanals, two median widest; subcaudals not modified; 12 lamellae under longest fingers; 17 under longest toes; those at base of toes somewhat tuberculate, distal ones flattened, usually without median keel.

Color: Dark brown above, with two series of blackish indefinite marks beginning behind shoulders, becoming larger posteriorly; toward back of body and base of tail they are practically transverse lines, interrupted mesially; on tail they form rather dim transverse marks, separated by very narrow lighter lines, more or less continuous with similar marks on side of tail; a narrow dorsolateral line evident anteriorly, vaguely evident posteriorly and on tail; a broad dark-brown stripe begins behind eye, continues along side of body and for some distance on tail, not surrounding ear. Labials bluish white with black dots; below lateral brown stripe, numerous blue-white markings and dots, together with black dots and flecks border venter; latter greenish-white in life, bluish in fixative, scales with lighter centers; mental white.

Measurements in mm.: Snout to vent, 71; tail partly regenerated,

74; snout to arm-insertion, 27; axilla to groin, 37, head width, 11.8; head length, 17; arm, 21; leg, 28.

Distribution: The specimens reported here are presumably the first to have been found in Thailand. These are from the following localities: Nos. 169, 226, 227, Coffee Camp, Na Bon, Nakhon Si Thammarat; 1430, Bukit Bayu, "Mt. of the sleeping Bhudda," Yala; 1384, Bukit Besar,* at waterfall near Na Pradoo, Pattani; Nos. 35751-35753, Khao Chong, Trang.

Remarks: The specimen figured (No. 35751, Khao Chong, Trang) is considerably larger than the described specimen and the dark coloration on the back and tail is less than described.

The behavior of the species is especially different from *Mabuya multifasciata* which is of comparable size. Specimens have not been seen moving about in the daytime but have invariably been dug out of dry soft earth under the edge of limestone rocks or from pockets of soil collected about buttresses of trees. They are surprisingly rapid in their movements, and most specimens routed from their hiding places escaped. Certain ones were found in dry dust under a high overhanging cliff. These were accidentally disturbed and both escaped. I returned next day and found both in the same small pocket of dust and both were captured.

This species has not previously been reported from Thailand.

Mabuya longicaudata (Hallowell)

FIG. 63

Euprepis longicaudata Hallowell, Trans. Amer. Philos. Soc., ser. 2, vol. 11, 1857, p. 77, pl. 4, fig. 1 (type-locality, Bangkok, Siam [restricted]).

Mabuia longicaudata: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 188; Stejneger, Bull. U. S. Nat. Mus., no. 58, 1907, pp. 214-215, pl. 16; Van Denburgh, Proc. California Acad. Sci., 1912, pp. 228-229; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, June, 1916, p. 55.

Eumeces siamensis Günther, Reptiles of British India, 1864, p. 91 (type-locality, Bangkok, Thailand [restricted]).

Mabuia siamensis: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 188; Flower, Proc. Zool. Soc. London, 1899, p. 647; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 84.

Euprepes (Tiliqua) rubstrati Fischer, Abb. Nat. Hamburg, 1886, p. 7, pl. 1, fig. 2 (type-locality, Formosa); Van Denburgh, Proc. California Acad. Sci., 1912, p. 229.

Euprepes (Tiliqua) bicarinatus Peters, Mon. Akad. Wiss. Berlin, 1867, p. 22 (type-locality, Hong Kong).

* The Malay name of this mountain is still used in the south. The mountain lies at the boundary of the provinces of Yala, Pattani, and Songkhla and embraces a part of each. Na Pradoo is situated about two kilometers from the extreme northeastern part of the mountain. The "waterfall" is about eight kilometers northwest of Na Pradoo. This mountain was first explored herpetologically by Annandale and Robinson, 1901-1902. At this time Pattani was divided into seven states: Rhaman, Jalor, Nawngchik, Tibaw, Jhering, Telubin, and Pattani. Certain new forms described from this area have been overlooked by certain writers, as being within the country of Thailand.

Mabuya longicaudata: M. Smith, The Fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 270-271; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, pp. 1109-1110.

Diagnosis: Large skink; dorsal scales with fine, usually wavy striations and two dim keels anteriorly, three evident near base of tail; lower eyelid scaled, lacking disc; a postnasal and supranasals; prefrontals form a median suture. Arms and legs well developed; leg reaching palm when arm is adpressed; 26-30 scales around body.

Description of species (from No. 33186, Sara Buri province): Rostral much broader than high, rather narrowly visible from above; supranasals form median suture; frontonasal broader than long, touching first loreal; prefrontals large, very narrowly separated mesially; frontal longer than wide, its length equal to its distance from tip of snout, and equal to combined parietals, touching frontonasal; nostril in posterior part of nasal, the posterior edge a narrow rim; a postnasal; anterior loreal higher than second, slightly higher than wide; posterior loreal longer than high; small preocular; two presuboculars; four supraoculars, second not or barely touching prefrontal, leaving two supraoculars touching frontal; six supraciliaries; seven supralabials, fifth below eye nearly twice as long as high; labial border of mental exceeding that of rostral; one undivided postmental; first chinshields in contact, second pair separated by one scale, third pair not greatly enlarged, separated; ear-opening small with three rounded lobules projecting from anterior border; four somewhat enlarged preanal scales.

Arms and legs well developed; digits covered below with flat lamellae, about 17 under longest fingers, 24-25 under longest toes; leg when adpressed reaches palm of hand, or a little farther.

Scales around body subequal, nearly or completely smooth on temples and neck; dorsal scales striate usually with two dim obtuse keels; scales on tail with three more or less well-defined keels; ventral and many laterals scales smooth; 28 scales around middle of body; 47 transverse scalerows from parietal to above vent; tail regenerated.

Color: Nearly uniform brownish or brownish-olive above with the head a little darker; broad dark-brown to black lateral stripe covering three scalerows; below, this margined dorsolaterally by a light line composed of small ill-defined dots; labials greenish with some black flecks; venter nearly uniform yellow-green, at times approaching canary-yellow; sole, palm, and underside of digits brown.

Measurements in mm.: Snout to vent, 117; tail, regen.; head

FIG. 63.—*Mabuya longicaudata* (Hallowell) No. 34240, Bang Saen, Chon Buri, Thailand. About natural size.

width, 11; head length, 26; arm, 31; leg, 43; snout to ear, 21; snout to arm, 39; axilla to groin, 56.

Variation: This is one of the larger species of *Mabuya*, the tail usually measuring nearly twice the snout-vent length. The subcaudals are 127 and 128 in two Thai specimens. The number of scales around the middle of the body is usually 28 although 26 and 30 have been reported. Transverse scalerows from parietal to above vent vary between 47-49.

One specimen examined shows a wider dorsolateral light line (bluish white) covering one and one-half scalerows. There are seven dim dark lines visible on dorsum. Another shows the dorsolateral light line invaded by black above and below thus leaving a line bordered above and below by blackish triangular dots for a part of its length.

In the young, the lateral stripe is deep black and there are no white dots in evidence. The dorsal color is nearly uniform.

Distribution: The records for Thailand suggest that the species is widespread, probably occurring in most of the continental portion of the country and at least a part if not all of the peninsula. I have taken or examined specimens from the following provinces: Chaiyaphum, Chiang Mai, Rat Buri, Nakhon Phanom, Udon Thani, Chon Buri, Sara Buri, and Phatthalung.

Outside of Thailand the species is known in southern China, Indo-China, Hongkong, Hainan, and Formosa. It has also been found in Malaya but apparently in only a few places (Pahang and Pulao Tioman).

Mabuya rugifera (Stoliczka)

Fig. 64

Tiliqua rugifera Stoliczka, Journ. Asiat. Soc. Bengal, vol. 39, 1870, p. 170, pl. 10, fig. 3 (type-locality, Camorta, Nicobar Islands).

Mabuia rugifera: Boulenger, Catalogue of the lizards of the British Museum, vol. 3, 1887, p. 184; The fauna of British India, Ceylon and Burma; Reptilia and Batrachia, 1890, p. 190; Flower, Proc. Zool. Soc. London, 1899, p. 645; M. Smith, Ann. Mag. Nat. Hist., ser. 9, vol. 18, 1926, p. 78.

Mabuya rugifera: M. Smith, The fauna of British India, including Ceylon, and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, p. 273.

Euprepis (Tiliqua) percarinatus Peters, Mon. Akad. Wiss. Berlin, 1871, p. 571 (type-locality, Matang, E. Java).

Euprepis percarinatus borneensis Peters, Monatsb. Akad. Wiss. Berlin, 1871, p. 572 (type-locality, Sarawak, Borneo).

Mabuia quinquecarinata Werner, Verh. Zool.-bot. Ges. Wien., vol. 46, 1896, p. 12 (type-locality, Sumatra).

Diagnosis: Prefrontals separated; interparietal very small, with parietals in contact behind it; one pair of nuchals; lower eyelid

scaly; dorsal scales generally quinquecarinate, laterals sometimes with seven strong keels; 24-28 scalerows around body; five to seven longitudinal greenish-white lines on body (or none); lines often broken.

Description of species (from No. 1526, La Doo Tin Mine, Bendang Stah, Yala): Rostral two and one-half times as wide as high, rather

FIG. 64—*Mabuya rugifera* (Stoliczka). Br. Museum No. 1934.7.6.1, Gunong Kledang, 2646 ft. Perak; about natural size.

truncate posteriorly, broadly in contact with frontonasal; small slender supranasals widely separated; frontonasal about as broad as long, or a little broader, forming suture with frontal; prefrontals separated; frontal seven-sided, longer than its distance from tip of snout, approximately as long as distance to nuchal; two frontoparietals; interparietal small; parietals large, in contact behind interparietal, keeled posteriorly; nuchals small, more or less distinct; nostril in single nasal; no postnasal; first loreal twice as high as wide; second loreal lower, one and one-half times as long as high; two presuboculars; supralabials 9-9, sixth three times as long as other supralabials; four supraoculars, second touching or somewhat separated from prefrontal; six clearly defined supraciliaries, separated from rather large palpebral scales by three or more rows of fine granules; lower palpebrals smaller than upper, bordering a series of three or four larger shields on eyelid; latter separated from sixth labial by five rows of small granules; three or four superimposed pairs of temporal scales strongly keeled; auricular opening a longitudinal oval with some tiny lobules above.

Mental with labial border greater than that of rostral, truncate behind, followed by a broad postmental; this in turn followed by four pairs of chinshields; first pair forms a suture, second and third separated by one scale, fourth small, last two pairs not touching labials; seven infralabials.

Twenty-four scalerows about middle of body, dorsal and lateral scales subequal, with three to six strong keels, some of which form mucrones, leaving scales notched posteriorly; 24 scales about neck; 31 transverse rows from nuchals to above vent; eight ventral rows smooth; a pair of large preanals, flanked by two small lateral scales; subcaudal scutes a little wider and larger than adjoining scales.

Arm moderate; leg adpressed, reaches beyond elbow of arm; small irregular scales in axilla; 19 lamellae under longest finger, proximally flat, wide distally, compressed; a prominent tubercular scale on wrist; toes with lamellae similar to those on hand, about 24 under fourth toe.

Color in life: Above dark-olive; sides of head somewhat brownish; labials yellowish cream; venter greenish white; blackish under digits.

Measurements in mm.: Snout to vent, 59; tail broken; width of head, 9; length of head, 14; snout to arm-insertion, 20.2; axilla to groin, 30; arm, 18.5; leg, 27.

Variation: A postnasal may be present, the sixth labial may be divided by a vertical suture; the dorsal scales usually have five

keels, with seven keels on sides. In the described specimen occasional scales may have six keels dorsally and laterally, while the outer keeled rows may have only three or four; the species may have five to seven greenish-white lines or the lines may be broken into a series of spots. Other specimens may be uniform olive; these are usually if not invariably males.

Distribution: Rugifera has been reported in Thailand only at Benang Stah, Yala. My specimens come from the same amphur (county). Two other specimens seen, escaped. They were along the edge of a tiny rivulet.

Outside of Thailand the species is known in the Nicobar Islands (the type-locality), Malaya, Sumatra, Java, and Borneo.

Remarks: The figure shows a specimen of the lined phase, B.M. No. 1934.7.6.1. from Gunong Kledang, 2646 ft. Perak the adjoining Malay state. This differs from the described specimen as follows: There are 26 scalerows about the middle of the body; the first loreal is broken transversely on one side; the second supraocular is separated from the prefrontal; five supraciliaries present; no nuchals; while 26 lamellae are present on the underside of the fourth toe.

Mabuya multifasciata (Kuhl)

FIG. 65

Scincus multifasciatus Kuhl, Beitr. Zool. und Vergl. Anat., 1820, p. 126 (no type-locality recorded; fixed by Taylor and Elbel, Batavia, Java).

Mabuia multifasciata: Fitzinger, Neue Klassification der reptilien . . . 1826, p. 52 (type-locality, Java); Boulenger, Catalogue of the lizards in the British Museum (Natural History), vol. 3, 1887, p. 186; Anderson, Journ. Linn. Soc., vol. 21, 1889, pp. 334-335; Boulenger, The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, pp. 191-193; Laidlaw, Proc. Zool. Soc. London, 1901, pt. 1, p. 310; Mocquard, Les reptiles de l'Indo-Chine, 1907, p. 38; Boulenger, A vertebrate fauna of the Malay Peninsula, . . . Reptilia and Batrachia, 1912, p. 84; Flower, Proc. Zool. Soc. London, 1899, p. 645; Annandale, Journ. Asiat. Soc. Bengal, ser. 2, vol. 2, 1905, p. 141; Smith and Kloss, Journ. Nat. Hist. Soc. Siam, vol. 1, no. 4, 1915, pp. 242-243 (varieties and localities); M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, Dec. 1916, p. 156 (peninsular Siam); *ibid.*, June 1916, p. 55; de Rooij, Reptiles of the Indo-Australian Archipelago, vol. 1, Lacertilia, Chelonia, Emydosauria, 1915, pp. 162-163, fig. 69; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 420; Pope, Bull. Amer. Mus. Nat. Hist., vol. 58, 1929, p. 377; Kopstein, Treubia, vol. 11, 1930, p. 307; Weekes, Proc. Linn. Soc. New S. Wales, vol. 55, 1930, p. 560.

Mabuya multifasciata multifasciata: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 268-269.

Euprepes sebae Duméril and Bibron, Erpétologie générale, vol. 5, 1839, p. 692 (type-locality, Batavia, Java [restricted by M. Smith, 1935]).

Tropidolepisma macrurus Bleeker, Naturg. Tijdschr. Nederl. Ind., vol. 20, 1860, p. 328.

Mabuia monticola Annandale, Journ. Asiat. Soc. Bengal, ser. 2, vol. 1, 1905, p. 143.

FIG. 65.—*Mabuya multifasciata* (Kuhl). No. 33539, Kanchanaburi, Kanchanaburi province, Thailand. Actual snout-vent length, 90 mm. Total length, 248 mm.

Plestiodon sikkimensis Gray, Ann. Mag. Nat. Hist., ser. 2, vol. 12, 1853, p. 388 (type-locality, Sikkim).

Diagnosis: Supranasals touching or slightly separated from each other; a postnasal; prefrontals in contact; first loreal not higher than second; no disc in lower eyelid. Scales usually tricarinate, rarely more; 30-34 scalerows about middle of body; usually dim, dark, dorsal lines between scalerows; sides dark brown usually with numerous ocelli.

Description of species (from No. 33539, taken at Kanchanaburi): Rostral not quite as broad as high, touching frontonasal narrowly; supranasals narrowly separated, each touching postnasal and first loreal; frontonasal much broader than long; prefrontals broadly in contact; frontal as long as its distance from tip of snout; four supraoculars, second, touching prefrontal, largest; frontoparietals paired (one broken abnormally), interparietal small, not enclosed by parietals; a pair of enlarged nuchals; nostril in posterior part of nasal separated from supranasal and postnasal by a very narrow rim; anterior loreal no higher and but little smaller than second; first touching one supralabial, second, two; three very small preoculars; two presuboculars; six supraciliaries; three postsuboculars; three anterior and three secondary temporals; seven supralabials, fifth elongated, below eye; six infralabials; mental border on mouth longer than rostral border; one broad postmental; first chinshields broadly in contact, second pair separated by one scale, third pair elongate separated by five scales. Lower eyelid with several semiopaque scales; ear-opening large with four or five auricular lobules on anterior border. Dorsal scales distinctly tricarinate, not striated or forming continuous lines; temporal scales nearly smooth; lateral scales tricarinate growing less distinctly keeled low on sides; ventral scales smooth. Caudal scales keeled on anterior half of tail, growing smooth distally. Scalerows about middle of body, 34; around neck, 32; 45 transverse rows, between parietals and a point above vent; 90 subcaudals, median row wider than adjoining rows.

Arms and legs well developed, the leg reaching nearly to axilla when adpressed; 17 scales under fourth finger, 19-20 under fourth toe, scales compressed, with keels, small tubercles, or thickenings, near their bases.

Color in life: Above, olive-gray with narrow blackish lines bordering scalerows; somewhat indefinite light olive or yellowish-olive dorsolateral line; on side broad brown stripe, darkest on edges of dorsolateral light lines and growing light brown to gray-brown low

on sides; stripe with numerous black and greenish-cream ocelli continued onto tail; below on venter, grayish or greenish-white with a wash of yellow; labials greenish-white.

Measurements in mm.: Snout to vent, 90; tail, 158; head length, 23; head width, 13.7; snout to ear, 18; snout to arm-insertion, 34; axilla to groin, 48; arm, 28.5; leg, 39.8.

Variation: Rarely the supranasals touch, separating the rostral from the frontonasal. The postnasal seemingly is invariably present. The temporal scales may show low keels. Rarely five keels may be counted on dorsal scales, the lateral scales often showing low or indefinite keels. The scalerows vary between 30-34 around the body; the hind limb varies in its reach with age. Malcolm Smith records 125 mm. snout to vent length, and 180 mm. as tail length for the species. The male during the breeding season has a large orange or red-orange blotch in the axillary region, which may extend to the groin.

Distribution: The species is ubiquitous in Thailand, having been taken in practically every province where collecting has been done. Outside of Thailand the species spreads its range from southern China, Indo-China, Northeastern India, Assam, Burma, to Malaya, and the Indo-Australian Archipelago.

Remarks: This species has been treated by Malcolm Smith as having *Mabuya rudis* as a subspecies. Anyone who has found the two together in the field will probably not subscribe to this treatment. He states (Smith, 1935, p. 269) "This form [*M. m. rudis*] occurs also on Sumatra and on Mentawei Islands but not to the exclusion of the typical form."

Thus throughout much of the range *rudis* occurs with *multifasciata*. I have taken both together in Mindanao and certain of the Sulu Islands. Smith states that *M. multifasciata* is apparently not found on Borneo. He has overlooked a paper de Rooij (1915, p. 163) that reports *multifasciatus* from several Bornean localities, and also reports *rudis* from several of the same localities.

Multifasciata is an ovoviviparous species producing four to eight young at a time. It is primarily a lowland form.

Mabuya macularia (Blyth)

Euprepis macularia Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 652 (type-locality? Rangpur, Bengal); M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 264-266.

A considerable number of small forms of *Mabuya* have been

described from India. These include *brevis* Günther, *subunicolor* Blanford (as a variety), *madaraszi* Mehely, *dawsoni* Annandale, and *allapallensis* Schmidt.

Concerning these Doctor Smith (*l. c.*) says: "When a good series of this lizard from different parts of its range are compared it will be seen that five more or less distinct geographical forms can be distinguished. Aberrant individuals—those that resemble forms from one area but occur in another area—are to be found, but on the whole the combination of color-pattern and morphological characters can be relied upon."

The above listed species are placed in synonymy by Dr. Smith and then he proceeds to distinguish five "forms" one of which, No. 5, is reported as follows:

"Like no. 1 but the leg longer, sometimes reaching to the axilla, and with the light lateral stripes more distinct; throat sometimes spotted with black. Examples of this form from the islands of the Gulf of Siam (Koh Kut and Koh Phai) have 30, 32, or 34 scales round the body. From snout to vent, 65 mm."

There are three forms in Thailand that I have encountered which I consider subspecies of *macularia*. It is probable that the typical form does not occur here.

Mabuya macularia quadrifasciata Taylor and Elbel

FIGS. 66, 67

Mabuya macularia quadrifasciata Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1103-1105 (type-locality 1780 m. elev. Phu Nam Lang (Mt.) Ban Khok, Na Phung, Dan Sai, Loei, Thailand).

Diagnosis: Four dark dotted dorsal lines on back; scales on chin and throat with brown borders; most scales of sides each with a lighter area; an axillary pit or pocket; anterior loreal usually divided; area of specialized "chiggermite" scales on leg above ankle.

Description of subspecies (from CU. No. 2679, Phu Kading (Mt.) Loei province): Rostral considerably wider than high, well visible on top of snout, forming a curving suture with frontonasal; supranasals slender separated, as long as nasal; frontonasal as wide as long forming a curving suture with frontal, touching first loreal and supranasal laterally; prefrontals moderately large, separated; frontal elongate, slender, its length greater than its distance from tip of snout, much longer than its distance from nuchals; paired frontoparietals; interparietal not enclosed by short parietals; a pair of nuchals; nasal divided; no postnasal; anterior loreal higher and shorter than second; two preoculars; one pre-subocular; temporals,

3 + 3; seven supralabials, fifth largest elongate, below eye; lower eyelid scaled; six supraciliaries; four supraoculars, second not in contact with prefrontal; mental a little wider than rostral; large azygos postmental; two pairs of chinshields both separated from each other but touching infralabials; 30 scalerows around middle of body; ear moderate with two or three lobules; head scales, except nuchals, smooth; dorsal scales with five (usually) or six keels, median ones a little farther apart than outer; lateral scales with six or seven keels; scales on arms and legs with two or three keels; scales on chin, venter, subcaudal area, and underside of

Fig. 66.—*Mabuya macularia quadrifasciata* Taylor and Elbel. Type. EHT-HMS No. 31802, Namlang Mt. 1780 m. Loei province, Thailand. Actual snout-vent length, 57 mm.

limbs smooth; subcaudal scales widened except at base; tip of tail missing; six preanal scales moderately enlarged; a small chigger-refuge above ankle; eleven lamellae under two median fingers; 14 under longest toe. Limbs overlap when adpressed.

Color: Male. Above olive-brown with indefinite small black spots, each with tiny brown or whitish dots; a black stripe along

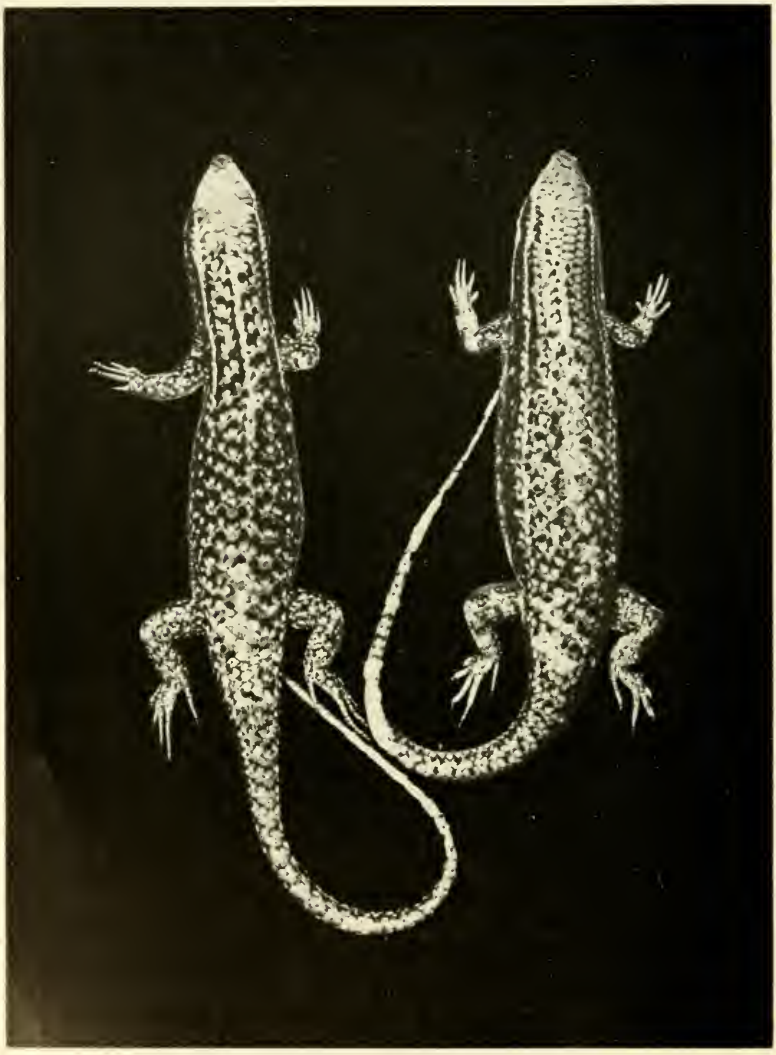


FIG. 67.—*Mabuya macularia quadrifasciata* Taylor and Elbel. Left figure No. 2679♂. Actual total length, 147 mm. Right figure No. 2678♀. Actual total length 138 mm. Both from Phu Kading, Loei province, Thailand.

side of head and body bordered by indefinite light dotted lines anteriorly. Sides of body and tail with very numerous small irregular black spots each with a white or bluish-white dot. Ventral scales of chin and throat bluish, most with a dark border; ventral scales ultramarine, smoky along edges; subcaudal area very light bluish gray.

Measurements in mm.: Nos. 2679 ♂, 2678 ♀; snout to vent 57, 58; tail 90 (tip missing), 80 (part regenerated); snout to arm-insertion, 22, 20; axilla to groin, 27, 30; width of head, 10.2, 10; length of head, 15, 14.5; arm, 15, 16; leg, 23, 22.

Variation: The female differs in having most of the dorsal scales with black spots tending to form rows anteriorly but no white dots; the cream-white dots on sides are fewer, smaller and less conspicuous than in the males; a dorsolateral light line (or row of white dots) from eye to midway on body; another line from below eye, at least to near insertion of arm; a dark lateral stripe from eye along side of body; sutures of labials black.

Distribution: This form is probably confined to the mountains of the eastern part of the Khorat Plateau.

Mabuya macularia postnasalis Taylor and Elbel

Mabuya macularia postnasalis Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1105-1106 (type-locality 2100 m. elev., Phu Lom Lo, Kok Sathon, Dan Sai, Loei province Thailand).

Diagnosis: A postnasal present; a specialized group of scales on leg above ankle forming a chigger-mite refuge; no axillary "chigger pocket." A dark lateral band present bordered below by a light line; a few scales on rump and those on lower lateral rows with small blackish spots some of which may have a tiny cream spot in center; one or two presuboculars.

Description of subspecies: A small species, limbs overlapping when adpressed; rostral and frontonasal touching; prefrontals narrowly separated from each other and touching the second supraocular; supranasals small, separated; anterior loreal single, higher but narrower than second; a true postnasal present; no scale behind supranasal; one presubocular; usually four enlarged palpebral scales; frontal about equal to its distance to the end of the snout, shorter than combined length of parietals; one pair of nuchals; seven supralabials; three primary and three secondary temporals; frontoparietal suture two thirds of the length of the scales, longer than the interparietal which separates parietals; eight infralabials; mental border on mouth wider than that of rostral; five supraciliaries; four supra-

oculars, two touching frontal; 30 scalerows around body; 15-16 lamellae under fourth toe; no shallow pocket in axilla; tail complete with 71 subcaudals; ear about half size of a dorsal scale, with some tiny lobules bordering the anterior edge.

Area above foot on leg with specialized pointed scales strongly infested with chigger-mites; scales of body three or five-keeled (sometimes seven-keeled), becoming four-keeled on base of tail the two inner keels stronger and a little wider apart, the median keel absent; scales not or scarcely denticulate behind; scales on sides of neck, on arm and leg, with two or three keels, more distinct on neck and leg. Ventrals smooth and lower lateral scalerows smooth or nearly so.

Two pairs of enlarged chinshields touching labials, first pair very narrowly separated, second pair separated by a scale; third chinshields small, separated from labials by an elongate scale; median preanals larger than outer ones; subcaudals slightly wider than adjoining scales.

Color: Above brown or brown-olive with a very dim darker lateral band on side, most distinct on neck, bordered above by a slightly lighter line scarcely visible behind neck; there are eight scales on back between darker bands; numerous small dark equal-sized flecks scattered on rump, each with a tiny lighter middle part; along lateral stripe all scales with a discrete black spot; below this

Measurements in mm. of *Mabuya macularia postnasalis*

NUMBERS	40109	40110	40111	40112
Length, snout to vent	58	55	56	55
Tail	.....	80	85	72 broken
Head length	15.5	14	15	.....
Head width	10.5	10.2	10.2	.....
Snout to ear	12.3	11.2	12	.....
Snout to arm	20.5	19.8	18	.....
Axilla to groin	29	25.5	24.4	25.2
Arm	19	18.2	17	16.8
Leg	25.5	22.5	23	23
Postnasal	Yes	Yes	Yes	Yes
Prefrontals separated	Yes	Yes	Yes	Yes
Prefrontal touches 2nd supraocular	Yes	Yes	No	Yes
First chinshields separated	Yes	No	Yes	No
Supraciliaries	5	5	5	5
Axillary pocket	No	No	No	No
Chigger "area" on leg	Yes	Yes	Yes	Yes
Scalerows	30	30	30	30

stripe all scales with black dots tending to form rows; one or two similar lines of dots along tail; a distinct light line from tip of snout along supralabials below ear (but including lower edge) and continuing very dimly along side below dark stripe; chin without dark marks; seven median ventral rows of scales uniform, probably white or yellow in life.

FIG. 68.—*Mabuya macularia malcolmi* Taylor and Elbel. No. 34701, Rice Experiment Station, Phatthalung, Phatthalung province. Actual total length, 122 mm.

Mabuya macularia malcolmi Taylor and Elbel

FIGS. 68, 68a

Mabuya macularia malcolmi Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, 1107 (type-locality, Phu Phak Khi Nak (Mt.), near Ban Nam Yen, Kok Sathon, Dan Sai, Loei province, Thailand).

Diagnosis and description: No trace of an axillary pit, no postnasal, but posterior part of nasal somewhat narrowed; frontal shorter than combined parietal but equal or a little greater than its distance from snout tip, wider than the frontonasal, but touching it; second loreal relatively short, much less than twice as wide as first loreal;

FIG. 68a.—*Mabuya macularia malcolmi* Taylor and Elbel. No. 2268, Doi Suthep Thailand, elev. 100 meters. About natural size.

a chigger mite refuge on the lower part of leg; leg adpressed reaches to elbow; first chinshields separated mesially; transverse rows of scales, parietal to above vent, 38; from mental to vent, 47; 30 scalerows about body.

Color: Above generally olive, each dorsal scale with a slightly darker central area; head darker olive; a dorsolateral stripe on side of head and neck continued on to the anterior part of body, and bordered below by a lighter line from the upper lip; four preanal scales whitish.

Genus DASIA Gray

Dasia Gray, Ann. Mag. Nat. Hist., vol. 2, 1839, p. 331 (type of genus, *Dasia olivacea*).

Diagnosis: Arboreal skinks, the palatine bones meeting on palate mesially; pterygoids in contact; palatal notch not reaching level of eyes; maxillary teeth conical; usually one or two pterygoid teeth; nostril pierced in a nasal; supranasals present; prefrontals, frontoparietals, and interparietals distinct; ear-opening small; tympanum deeply sunk; limbs well developed, pentadactyl.

Only a single species is known to occur in Thailand, and this only in the southern peninsula area.

A second species, a form with three keels, occurs in Malaya and some of the larger islands of the Indo-Australian Archipelago. This, too, may be looked for in Thailand.

Dasia olivacea Gray

FIG. 69

Dasia olivacea Gray, Ann. Mag. Nat. Hist., vol. 2, 1838, p. 331 (type-locality, Penang, Malaya); Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 21; M. Smith, A fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 277-278.

Euprepes olivaceus: Günther, Reptiles of British India, 1864, p. 80, pl. 10, fig. 17.

Tiliqua olivacea: Stoliczka, Journ. Asiat. Soc. Bengal, vol. 39, 1870, p. 172.

Lygosoma olivaceum: Boulenger, Catalogue of the lizards in the British Museum, 2nd ed., vol. 3, 1887, p. 251; The fauna of British India . . . Reptilia and Batrachia, 1890, p. 187; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore . . ., Reptilia and Batrachia, 1912, p. 91 (*part.*); M. Smith, Journ. Siam. Nat. Hist. Soc. Siam, vol. 4, 1920, p. 96 (Pulo Condore).

?*Euprepes ernestii* Duméril and Bibron, Erpétologie générale . . ., vol. 5, 1839, p. 696 (type-locality, Java).

Diagnosis: A rather large skink (115 mm. snout to vent), greenish to olive with a series of 13 transverse markings consisting of irregular rows of greenish white dots each edged in blackish olive. A pair of small supranasals, widely separated; prefrontals touching or

FIG. 69.—*Dasia olivacea* Gray. No. 34432, Bukit Besar Mt. near Na Pradoo, Pattani. Actual length, snout to vent, 108; total length, 265 mm.

narrowly separated; four supraoculars; preanals not or but slightly enlarged; interparietal not enclosed by parietals; one pair of nuchals; 28-30 scalerows around body.

Description of species (from 34432 Bukit Besar, Na Pradoo, Pattani): Rostral broader than high, broadly visible above, in contact with frontonasal; latter distinctly broader than long, barely in contact with frontal; prefrontals large, narrowly separated; frontal as long as its distance from end of snout, about equal to length of combined parietals; pair of small supranasals, widely separated; nostril in single nasal, which touches only one labial; two elongate loreals, posterior longest; two presuboculars; four supraoculars, two touching frontal; paired frontoparietals; parietals wide but rather short, not enclosing interparietal posteriorly; pair of nuchals; seven or eight supraciliaries; four or five enlarged translucent scales on lower eyelid; pair of anterior temporals; seven supralabials, fifth longest below eye; six infralabials; mental large, its border on lip larger than that of rostral; postmental (abnormally) divided; first chinshields in contact, second pair separated by a scale.

Scales on body rounded, imbricate; 30 scalerows about middle of body; scales on neck smooth, gradually developing keels, those on latter half of body with three major keels and often with one or two other keels on each side; on tail, keels present only at base; scales on sides of body smooth; scales on limbs keeled, strongly so on legs; preanals not or but slightly larger than adjoining scales; lamellae under digits widened, flattened on basal parts, 16 or 17 under longest fingers; 19 under fourth toe; five or six enlarged flat tubercles border heel (yellow in color); 85 subcaudals, most of median series widened.

Ear very small; head rather pointed; tail slender, tapering to a narrow tip; arms and legs overlap length of hand when adpressed.

Color in life: Above greenish with some bronze scales in dorsolateral areas; series of thirteen transverse bands of small irregular greenish-white ocelli bordered by black and extending low on sides; venter bluish green becoming more bluish in preservation; palms and soles amber; blackish on tail, with flecks of greenish white and brown, the distal portion of undersurface olive-brown, basal portion greenish or bluish green. Top of head dark-olive with four pairs of black dashlike marks in supraocular region.

Measurements in mm.: Snout to vent, 108; tail, 157; width of head, 19; length of head, 25; snout to ear, 21; snout to arm-insertion, 39; axilla to groin, 52; arm, 27; leg, 34.

Variation: Malcolm Smith (1935) notes the following variations: scalerows 28-30; the dorsal scales may have three, five, or seven keels. The lamellae under the fourth toe vary between 17 and 22.

The young specimens are dark, often nearly black, with narrow irregular silvery transverse bars on dorsum.

Distribution: Specimens of *Dasia olivacea* have been taken in the provinces of Yala, Pattani, and Narathiwat in Thailand. It also occurs on the island, Pulao Panjang, Thailand.

The species has been taken in Cambodia, Malaya, Borneo, Sumatra, Java, and the Philippines.

Remarks: The species is largely arboreal in habit. The specimen here described was captured in a tree growing near the base of Bukit Besar (mountain) close to Na Pradoo, Pattani province. I am convinced that previous authors have confused more than a single species under this name; a five-keeled form is reported from Pulo Condore (off coast of Viet Nam) and I have seen specimens of a species in Malaya having three-keeled scales. The latter differs also in numerous other characters and occurs together with the species I consider to be *olivacea*.

Genus Riopa Gray

Riopa Gray, Ann. Mag. Nat. Hist., first series, vol. 2, Jan. 1839; p. 332 (type *Lygosoma punctata*).

Diagnosis: The chief features of *Riopa* are as follows: Supranasals present, separate or sometimes fused or partially fused with nasal; frontoparietal single or paired; prefrontals present, separated or touching; tympanum small, deeply sunk; eyelids reduced in species with elongated bodies; lower eyelid scaly or with a transparent disc. Palatine bones meet on midline of palate; pterygoids touching anteriorly, palatal notch not reaching to level of eyes.

This genus has six known representatives in Thailand, all belonging to the section of the genus having the lower eyelid covered with scales, lacking a transparent disc.

The genus is widespread, some fourteen species occurring in southern and southeastern Asia. It also occurs in Polynesia, Australia and Africa.

Key to Species of Riopa in Thailand

1. A single frontoparietal 2
   Two frontoparietals 4
2. Limbs widely separated, the arm contained in axilla-to-groin distance 7-9 times 3

Limbs less widely separated, the arm contained in axilla-to-groin distance 3 to 4 times; 28-30 scalerows around body; 56-60 scales in a row between parietals and a point above vent. Maximum length known, 41 mm. ..... *frontoparietalis*

3. Arm-length, in axilla-to-groin distance 9 times; 40-42 scales about middle of body; 143 scales in a row between parietals and a point above vent ..... *haroldyoungi*

Arm-length in axilla-to-groin distance approximately 7.25 times; 30-34 scalerows about middle part of body; 88-98 scales in a line between parietals and a point above vent ..... *isodactyla*

4. Limbs when adpressed widely separated; the arm length in axilla-to-groin distance approximately 5 times; 32-34 scalerows about middle of body; 60-63 scales in a row from parietals to above vent, ... *koratense*

Limbs when adpressed separated by a distance about equal to length of leg; arm-length in axilla-to-groin length 3-3.5 times 5

5. Scalerows about middle of body 26-28; dorsal scales distinctly keeled, no black dorsolateral line or indistinct lineation on dorsal scales, ... *herberti*

Scalerows about middle of body 28-30; dorsal scales smooth (rarely dimly keeled); snout to vent 70 mm.; a blackish dorsolateral line, ... *bowringi*

Riopa koratense (M. Smith)

FIG. 70

Lygosoma koratense M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, May 1917, pp. 222-223, pl. —, fig. 1, 1a, 1b (type-locality "Lat Bua Kao, Dong Rek [Dong Paya Fai] mountains").

Riopa koratense: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia; vol. 2, Sauria, Feb. 7, 1935, p. 314.

Diagnosis: Distance between end of snout and arm-insertion, twice in axilla-to-groin distance or slightly more; internasals partially fused with nasal; scales smooth in 32-34 scalerows at middle of body; tail shorter than head and body. Distance between adpressed limbs about equal to length of leg.

Description of species (from No. 33374, near Muak Lek, Sara Buri, but in Nakhon Ratchasima): Rostral wider than high, part visible above considerably longer than suture between supranasals; latter scales fused to nasals anteriorly; frontonasal about twice as broad as long touching first loreal; prefrontals small, widely separated, leaving a broad suture between frontal and frontonasal; frontal a fifth longer than its distance from tip of snout; frontoparietal divided; interparietal small enclosed behind by parietals; no enlarged nuchal scales; nostril in lowest part of the combined nasal-supranasal scale, a suture running forward from first loreal to above nostril; first loreal higher and shorter than second; a pair of unequal

FIG. 70.—*Riopa koratense* (M. Smith). No. 33374, near Muak Lek, Sara Buri, but in adjoining province, Nakhon Ratchasima. Actual snout-to-vent length, 106 mm.; tail, 95 mm.

preocular scales, one presubocular; four supraoculars second largest; six supraciliaries first and last largest; eyelid with two rows of scales besides palpebrals; two postsuboculars.

First labial largest, thickened somewhat, as are other scales on front of snout; eight supralabials, that under eye (fifth) only slightly enlarged; two primary temporals, three secondary, the upper primary largest.

Mental thickened, with a much longer labial border than rostral; seven infralabials; a large azygos postmental; first chinshields in contact; second pair separated by a scale; third pair, not clearly differentiated, separated by several scales.

Ear-opening very small (1½ x 1 mm.) with two small lobules projecting from anterior border; 28 scalerows around neck; the scales subequal; 32 scalerows about middle of body; 63 transverse scalerows between parietals and a point above vent; 71 subcaudals the terminal scale sharply pointed. Vent bordered by seven scales, not or scarcely differentiated from adjoining scales.

Limbs short, pentadactyl; digits with lamellae compressed, forming a more or less continuous keel; nine scales under two longest fingers, 13-14 under fourth toe; tail tapering rather suddenly to a point.

Color in life: Violet-brown, the scales edged behind with darker brown with an indefinite darker spot at base; sides lighter than dorsum, while scales on venter grayish-white, somewhat darker than this under tail. Scales of head with slightly darker edges.

Measurements in mm. of *Riopa koratense*

	Type	33374	33380
Snout to vent	105	106	101
Tail	95*	95	93
Snout to ear	...	15	14
Snout to arm	...	30	30
Axilla to groin	...	64	61
Length of head	...	19	18
Width of head	...	13	13
Width of body	...	19	17
Arm	15	15	16
Leg	24	25	24

* Reported incomplete; the tails are complete on the specimens reported by me.

Variation: The scalerows about body vary between 32 and 34.

Distribution: M. Smith has reported four specimen from the type locality at Lat Bua Kao in Nakhon Ratchasima on the Eastern

slope of the Dong Rek Mountains. My three specimens are from the vicinity of Muak Lek.

Remarks: The type description records that the flanks are pale greenish yellow, and the venter is yellowish white; it also states that the nostril is between two nasals but this latter statement is correctly interpreted in a later work (Smith, 1935, p. 314).

The species is a burrowing form, one having been taken from under a flat rock, the other dug out of debris. Both of my specimens were taken about one mile west of Muak Lek in low limestone mountains. This locality is actually in Nakhon Ratchasima province while Muak Lek is in Sari Buri province.

Riopa isodactyla (Günther)

FIG. 71

Eumeces isodactylus Günther, Reptiles of British India, 1864, p. 93, pl. 12, fig. A (type-locality, Cambodia).

Lygosoma isodactylum: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 339; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, 1914, pp. 127-128, fig.; *ibid.*, vol. 2, 1916, p. 56.

Riopa isodactyla: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 317-318 ("Central Siam between Ayuthia and Paknam Po, Nakhon Sawan").

Squamicilia [isodactyla] Mittleman, Smith. Misc. Coll., vol. 117, 1952, p. 9.

Diagnosis: Frontoparietal single; 88-98 transverse scalerows between parietal and a point above vent; internasal fused with nasal anteriorly; 30-34 longitudinal scalerows around body; ear-opening partially covered with scales; scales cover lower eyelid; first supralabial largest; legs small, pentadactyl, three median fingers subequal; three median toes subequal; tail somewhat shorter than head and body; eight dorsal scalerows, each scale dark-edged; a light band on occiput widening laterally; dark nuchal band terminating at ear-opening; remainder of side and venter yellowish.

Description of species (from No. 33185, Sara Buri): Head rather flat above and rather narrowed at tip of snout; rostral about as high as wide, well visible above forming narrow suture with frontonasal thus separating supranasals; supranasals fused anteriorly with nasals; no postnasal; frontonasal wider than long, touching single loreal laterally; prefrontals small, widely separated; frontal little longer than wide, little longer but less wide than single frontoparietal (partially divided anteriorly); interparietal small, enclosed posteriorly by large elongate parietals; latter bordered by three temporals and two small median scales; no enlarged nuchals.

Anterior loreal higher but narrower than second; latter little

FIG. 71.—*Riopa isodactyla* (Günther). No. 33185, near Sara Buri, Sara Buri province, Thailand. Actual total length, 148.5 mm.

longer than high; two preoculars; five or six suboculars; lower eyelid with seven scales, without a transparent disc; seven supraciliaries, last larger than first; four supraoculars, first two touch frontal; prefrontal touches first supraocular.

Seven supralabials, first largest, fourth, fifth and part of sixth below eye, subequal; three anterior temporals, upper touching parietal; four secondary temporals; mental much wider than rostral; six infralabials; an undivided postmental; first pair of chinshields in contact; second pair separated by one scale, third pair by three scales, but not touching infralabials.

Ear-opening separated from mouth-angle by a series of six or seven scales, almost obliterated by two large scales which cover much of the opening; tympanum deeply sunk; scales smooth, shiny, imbricate, in 32 longitudinal rows around body, and 98 transverse rows between parietals and a point above vent; 83 subcaudal scales, median not enlarged.

Arms and legs small, pentadactyl, clawed, distance between adpressed limbs equal to more than three times length of arm. Three middle fingers subequal; three middle toes subequal, the lamellae compressed, keeled, nine or ten under fourth toe; preanal region bordered by six scales.

Color in life: Head black on top with a few lighter points in front and behind interparietal and on front border of frontal; supralabials and infralabials each with a black spot; narrow light band across occiput, widening much on sides; black transverse band on occiput running between ears, narrowing laterally; back dark olive, scales strongly edged with black; sides similar except for a few fine punctations (more prevalent on sides of tail); chin, venter, and underside of tail yellowish; black spot on postmental with very few fine flecks on chinshields; underside of digits blackish.

Measurements in mm.: Snout to vent, 82.5; tail, 66; snout to ear, 10.3; snout to foreleg, 20; axilla to groin, 58; arm, 8.1; leg, 12.4; head length, 11.7; head width, 7.7; body width, 7.7.

Variation: The number of scalerows varies between 30 and 34, the type having only 30. The amount of black spotting varies considerably in specimens from the same or nearby localities.

Distribution: The species is known in Thailand from the provinces of Ayutthia, Sara Buri, and Nakhon Sawan.

The type-locality is Cambodia, and presumably is not known elsewhere outside of Thailand.

Malcolm Smith reports on nine specimens: Stone quarries at Sanam Cheng (north of Lopburi [2]); Lopburi [1]; Sam Kok [2]; Chong Kae (beneath stacks of firewood in the station yard [4]).

Remarks: The specimen described was taken from under a small log lying in an open field. It was very active and moved in a snake-like manner, the legs apparently not being used when moving fast.

A figure is given by M. Smith (1914). His color description follows: "Above dark yellowish thickly powdered with very dark brown, this color often confluent and forming patches. In one of these, the patches were so extensive as to practically obscure the ground color. Sides with a dark edge to each scale, forming oblique lines upwards and backwards. Below, pale yellow or yellowish-white speckled irregularly with brown. In the only half-grown specimen I obtained the belly was a uniform pale yellowish color. Labials, the first excepted, barred with yellow and brown alternately."

Riopa haroldyoungi Taylor

Fig. 72

Riopa haroldyoungi Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, p. 242-244, fig. 12 (type locality, Doi Suthep, Chiang Mai province).

Diagnosis: Skink with an elongate body, distance between tip of snout and insertion of arm contained in axilla-to-groin measurement about three and one-third times; length of arm in axilla-to-groin distance about nine times; ear-opening small distinct; nostril in nasal, almost bordering supranasal; rostral, first supralabials, mental, first infralabial, nasals, and supranasals somewhat thickened, bluish to ultramarine in color; first supralabial twice as large as three subsequent supralabials.

An ivory-white ring about head behind parietals; body with 32 irregular transverse light bands often broken, sometimes tending to form reticulations.

Description of species (from type): Body greatly elongated, adpressed limbs widely separated; head moderately large, scarcely as wide as body in postaxillary region. Tip of snout rounded; rostral large, distinctly visible above, posteriorly forming an angle; internasals completely free from nasal, subtriangular in shape, in contact mesially; frontonasal much wider than long, laterally in contact with anterior loreal; frontal relatively short (4 x 3.7 mm.), its broad contact with frontonasal nearly a straight line; prefrontals small, widely separated, touching both loreals; a single large fronto-

parietal, wider than long (5 x 3.5 mm.), notched posteriorly by small interparietal; parietals elongate (6 mm.) diagonally placed, not or barely enclosing interparietal; no distinct nuchals; nostril in single nasal, nearly twice as long as high; two loreals, anterior highest; four supraoculars, anterior triangular, second largest, fourth

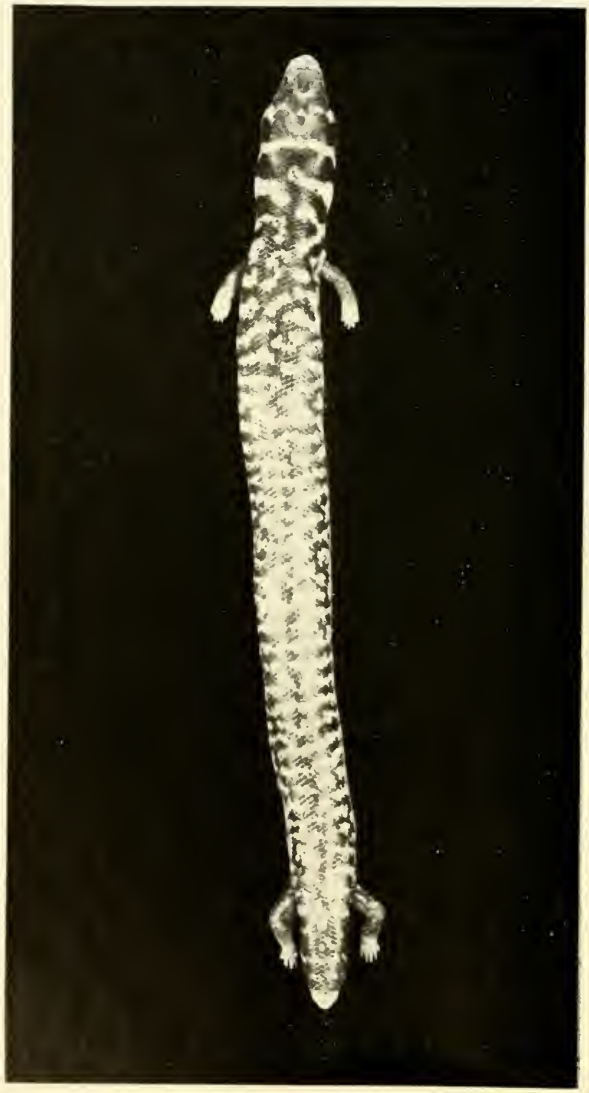


FIG. 72.—*Riopa haroldyoungi* Taylor. Type. From Taylor, Univ. Kansas Sci. Bull., vol. 43, no. 7, 1962, fig. 12. Actual length, 150 mm.

barely touching parietal; six superciliaries, five subocular and preocular scales; upper eyelid greatly reduced, lower lid with at least three rows of small scales.

Nine supralabials, anterior twice as large as any other labial, in contact with anterior loreal behind nasal; three rather enlarged temporals border parietal; mental with a larger labial border than rostral, partially fused to first infralabial; nine or ten infralabials, first largest; an azygos postmental; first chinshield in contact (partly fused), touching labials on one side only; second pair of chinshields separated by two or three scales and also separated from labials by one scale; third pair of chinshields scarcely differentiated.

Ear-opening small, distinct, upper anterior part partially covered by an overhanging scale or scales; limbs short. Arm pentadactyl, clawed, three median digits subequal, their length with claw, measuring about 1.5 mm., twice length of two outer digits; subdigital lamellae five or six; palm with rounded or flattened tubercles; four outer toes longer than inner, strongly curving, with strong well-developed claws; six and seven lamellae under longer toes; tympanum very deeply sunk.

Forty-seven smooth scales in a row about neck; 40-42 scalerows about body at middle; vent bordered anteriorly by ten slightly differentiated scales; basal subcaudals not enlarged or differentiated, greater part of tail missing with regeneration recently begun; 143 scales in a row from parietals to a point above vent.

Color in life: Generally dull black and yellowish ivory; snout-tip rather grayish ultramarine over the thickened scales; head blackish above with slight clouding of ivory-white; two ivory marks on chin run back, then up on side of head to eye; this followed by a similar dark band also proceeding to eye; next ivory band reaches front of parietal; followed by a black band, narrow below, but widening on temporal region; next ivory band encircles head behind parietals; from here on alternating bands are dull blackish and dirty ivory, often broken, sometimes tending to form reticulations; limbs somewhat darker, the light flecks indistinct.

Measurements in mm.: Snout to vent, 136; tail lost (regeneration begun), 14; snout to arm-insertion, 29; axilla to groin, 97; arm, 11; leg, 12; width of head, 12; length of head, 18; snout to ear-opening, 16; snout to arm-insertion in axilla-to-groin distance, 3.35 times; distance between adpressed limbs equals slightly more than 6.5 times length of arm; greatest body width, 13.6.

Remarks: Only the type is known. It was taken at the base of

Doi Suthep Mountain by Mr. Harold Young. It was kept alive at his zoo for some days but in trying to escape it fell in a water tank and was drowned.

The species is named for its discoverer.

Riopa herberti (Smith)

FIG. 73

Lygosoma herberti M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 45, fig. 2, pl. (type-locality, Nakhon Si Thammarat Mts., peninsular Thailand); *ibid.*, p. 55; Bull. Raffles Mus., no. 3, 1930, pp. 35-36.

Riopa herberti: Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 18; M. Smith, Fauna of British India including Ceylon and Burma . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 317 (Isthmus of Kra to Phuket).

Sphenosoma hughi Cochran, Proc. Biol. Soc. Washington, vol. 40, 1927, p. 185 (type-locality, Koh Tao, Gulf of Siam).

Riopa hughi: Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 18, fig. (Ban Hui Ta, Nakhon Si Thammarat).

Diagnosis: Distance between end of snout and insertion of arm, contained 1.75 times in axilla-to-groin distance; 26-30 scalerows around middle of body; 55-56 scales in a line between parietals and a point above vent; dorsal scalerows quinquecarinate.

Description of species (from No. 35692, Ronpibon, Tonka Harbour Tin Mine): Body not especially elongate; head not or slightly distinct from neck; rostral extending onto dorsal surface of snout, separated from frontonasal by supranasals, its posterior border curving rather than angular; frontonasal nearly twice as wide as long; supranasals subtriangular, mesially in contact; frontonasal forming a broad suture with frontal, widely separating small prefrontals; frontal longer than wide (3.8 x 2.5 mm.), anterior suture sinuous, the posterior curving; two frontoparietals each larger than interparietal; latter enclosed by the diagonally placed parietals. No distinct nuchals, scales of first row touching parietals a little larger than scales on neck, the two temporals being largest; nostril in a single nasal, its area greater than the part of the scale preceding or following it; two loreals, anterior higher and narrower than second; four supraoculars the first and second subequal in area, second touching frontoparietal, fourth touching parietal; seven superciliaries; seven well-defined supralabials; first larger than the three scales following but smaller than sixth; six infralabials; mental with a larger labial border than rostral; an azygos postmental; first chinshields touch; second pair separated by a scale, third and fourth scarcely differentiated, widely separated; all chinshields bordering infralabials; 28 smooth scalerows about narrow point of neck; 30 scalerows about middle of body; 57 scales in a row from parietals

to a point above vent; scales in nuchal region smooth; farther back most dorsal scales quinquecarinate. Lateral scales dimly carinate; ventrals smooth. Caudals di- or tricarinate on basal half; 86 subcaudal scales.

Limbs well developed; adpressed limbs fail to meet by a distance about equal to length of arm; fingers rather elongate, third and

Fig. 73.—*Riopa herberti* (Smith). Left figure No. 35524. Middle figure No. 35692. Right figure No. 35694. Tonka Harbour Tin Dredging Co., Ronpibon, Nakhon Si Thammarat. All approximately natural size.

fourth subequal in length; 12 lamellae under third and fourth fingers, basal ones elevated, rounded, distal ones compressed; palm covered with flattened tubercles; 15 lamellae under fourth toe, the distal ones compressed, the three middle fingers and toes with metacarpals and metatarsals bound together and separated from inner and outer toes.

Color: Dorsal color light tan the scales outlined with darker brown suggesting a continuous reticulum. Side of head darker, especially behind eye and on sides of neck, the color tending to be heavier on scale borders, some of which have lighter centers forming whitish flecks. Remainder of sides slightly darker than dorsum; venter unicolor.

Measurements in mm. of *Riopa herberti*

NUMBER	35472	35524	35692
Snout–vent length	66	56	60
Tail length	51*	71	52*
Head width	9.3	8	9.6
Head length	13.4	13	15
Snout to arm	20.3	19.2	21
Axilla to groin	36.5	31	33
Arm length	12	11.3	13
Leg length	17	17	17

* Regenerated. Nos. 35472, 35524 are from 5-7 km. west of Nakhon Si Thammarat. No. 35692 from near Ronpibon in the same province.

Variation: There is some variation in the distinctness of the stripe from eye along side of body. In some it is a distinct dark stripe to groin, while in others it can scarcely be distinguished beyond the neck. Usually small whitish flecks are evident on the neck, and sometimes also on the side. One specimen, No. 35694, from near Ronpibon had a bright red tail. There is a slight pattern evident on the venter, the edges of the scales being very slightly darker but this is visible chiefly after preservation.

On the regenerated tail the scales are darker with some transverse marks indicated. Two specimens from Na Bon differ from the Ronpibon specimens in having only six supralabials, the fourth being the subocular. These are darker than most southern specimens.

Distribution: In Thailand the species has been taken in the province of Nakhon Si Thammarat; at Klong Tun Sai in Phuket; at Nam Chik, Pak Chan Estuary, Chumpon.

Remarks: M. Smith has synonymized Dr. Cochran's *Riopa lughi*

from the Island Koh Tao (turtle island) with *herberti*. I have examined the type and concur in the synonymy. My series of *Riopa herberti* show some variation in the characters mentioned by Dr. Cochran as separating the two forms.

M. Smith reports a specimen measuring 67 mm.

Riopa bowringi (Günther)

FIG. 74

Eumeces bowringi Günther, The reptiles of British India, 1864, p. 91 (type-locality, Hong Kong).

Lygosoma bowringi: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 308, pl. 13, fig. 3; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 320; Flower, Proc. Zool. Soc. London, 1899, p. 650.

Lygosoma comotti Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 4, 1887, p. 622; Fauna of British India, Ceylon, and Burma; Reptilia and Batrachia, 1890, p. 207 (type-locality, Minhla, Burma).

Riopa bowringi: Smith, Fauna of British India including Ceylon and Burma . . . Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 315-316.

Diagnosis: Distance between snout and arm-insertion contained 1.5 times in axilla-to-groin distance; a pair of nuchals present; lower eyelid scaly; usually 28-30 scales around body; tail 1.75 times length of head and body; dorsal scales smooth (rarely dimly keeled); a blackish dorsolateral line.

Description of species (from No. 34325, Bang Saen, Chon Buri province): Rostral moderately large well visible above, its posterior border slightly angular; internasals in contact mesially, touching anterior loreal; frontonasal large, laterally touching first loreal; prefrontals widely separated, the suture between frontal and frontonasal nearly a straight line; length of frontal greater than its distance from tip of snout, less than length of combined parietals and frontoparietals; frontoparietal divided; interparietal enclosed by parietals; one pair of well-developed nuchals; nostril in a single nasal; two loreals, anterior higher and narrower than second; four supraoculars second largest; six supraciliaries; six or seven infralabials; border of mental on lip slightly greater than that of rostral; a large azygos postmental; three pairs of chinshields, first in contact, second pair separated by a scale, third separated by five scales, all pairs bordering infralabials. Two large anterior temporals; scales in 30 rows around neck, 31 rows about middle of body; scales in nuchal region definitely widened, ventral scales larger than laterals but smaller than dorsals; limbs when adpressed fail to touch by a distance equal or slightly greater than length of arm; eleven lamellae under longest fingers; 16 under longest toe; none or a single low projecting lobule from upper anterior border of ear-opening.

Color in life: Above honey-brown with a pair of indefinite dorsolateral light cream or light tan lines, bordered laterally by a narrow black line running to groin; six median dorsal rows of scales, each scale with a short median bar which together tend to form lines on the back, the two median and the two outer lines being most distinct; a dorsolateral black stripe continued along tail as an in-

FIG. 74.—*Riopa bowringi* (Günther). Left figure, No. 34325. Ang Hin, Chon Buri province, Thailand. Actual total length, 102.5 mm. Right figure, No. 34281, Bang Saen, Chon Buri province, Thailand. Actual total length, 91 mm.

distinct dotted line; a continuous light line along supralabials with black dots or flecks above and below. Sides of neck and body punctate with black and cream-yellow to ivory-white; chin venter and subcaudal region yellow-ivory.

Measurements in mm.: Snout to vent, 47.5; tail complete, 55; snout to arm-insertion, 17; axilla to groin, 26.5; head width, 7; head length, 11; arm, 8; leg, 13.

Variation: Occasional specimens show slight carination, and I believe this is the condition in the type. A race in the Andaman Islands has tricarinate scales. There are 26-30 scales around the body, and from 52 to 58 from parietals to above vent. There are 10 to 15 lamellae under the fourth toe. A review of the populations throughout the wide range will doubtless show the presence of certain forms that should be distinguished as subspecies.

Distribution: The species occurs widely in Thailand. Specimens have been taken in Chon Buri, Chanthaburi, Loei, Ubon, Udon Thani, Chiang Mai, Prachuap Khiri Khan, Chumphon, Nakhon Si Thammarat, Songkhla, Phatthalung, Pattani, Trang and Yala.

It ranges widely outside of Thailand in Hongkong (the type-locality), Indo-China, Burma, Malaya, Indo-Australian Archipelago as far as Palawan, Philippine Islands.

It is primarily a lowland form but I have taken it at elevations slightly less than 1000 feet. M. Smith reports it at 5,000 ft. in Annam!

Riopa frontoparietalis Taylor

FIG. 75

Riopa frontoparietalis Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 239-242, fig. 11 (type-locality, Hills near Scout Camp, Sara Buri, Sara Buri, Thailand).

Diagnosis: Similar to *Riopa bowringi* except smaller (snout to vent, 41), usually darker brown with frontoparietal single.

Description of the type: Rostral wider than high, visible above; a pair of supranasals forming a short median suture, touching nasals and anterior loreal laterally, about twice as wide as long; prefrontals quadrangular, widely separated, touching both loreals; frontal truncate anteriorly, longer than its distance to tip of snout, shorter than its distance to nuchal; frontoparietal single, much larger than interparietal touching three supraoculars; parietals forming a suture behind the interparietal; a pair of nuchals; nasal seemingly completely divided without separate postnasal; two loreals, anterior the higher, posterior slightly larger and subquad-

FIG. 75.—*Riopa frontoparietalis* Taylor. Type. No. 1694. Boy Scout Camp, near Sari Buri, Sara Buri province, Thailand. Actual total length, 85 mm.

rangular; two presuboculars, three postsuboculars connected by a row of tiny scales on lower edge of eyelid; eyelid covered by several scales; two large anterior temporals; three secondary temporals; supralabials, 7-7, fifth below eye; first larger than the three following; seven supraciliaries; mental with an oral border much larger than rostral; one undivided postmental, followed by a large pair of chinshields in contact; a second pair separated by five scales; six infralabials; ear-opening moderate, the anterior border with two lobules; scalerows about neck, 28; about middle of body, 28.

Scales from nuchal to above vent, 56; when arms and legs are adpressed they are separated by five scales; middle finger extends a little farther than fourth, the latter with ten subdigital lamellae; fourth toe longest, with 13 lamellae, tubercular proximally, compressed distally; six preanal scales, two median a little larger than others, and white in color; median subcaudal scales slightly enlarged, 78 in all.

Color in life: Above dark brown, head nearly uniformly colored above; pair of light brown dorsolateral lines, covering part of two or one whole and two half-rows of scales; six median, brown scalerows each row with a dim dark line. Side with a black line bordering dorsolateral light brown line below which side of neck and body covered with irregular vertical rows of dark brown and cream scales. Central part of supralabials with an indistinct cream line. Chin and ventral surface of body dirty white; underside of tail, gray; median anal scales pure white. Palm, sole, and underside of digits blackish.

Measurements and data of *Riopa frontoparietalis*

NUMBER	1694	33341	33342	33391	33392	33393
Snout to vent	38	33	35	41	41	36.2
Tail	47	38	41.5	55		42
Head width	6.1	6.5	5.4	6.3	6.4	6
Head length	9.4	8.5	9	10.4	9.3	9.5
Arm	8	6	7	8	8.2	8
Leg	10.3	7.5	9.5	12	11.2	11
Scales nuchal to vent	56	59	60	57	59	60
Scales around middle	28	30	30	28	28	30

Genus TROPIDOPHORUS Duméril and Bibron

Tropidophorus Duméril and Bibron, Erpétologie générale . . ., vol. 5, 1839, p. 556 (type of genus, *cocincinensis*).

Diagnosis: Palatine bones in contact in middle line of palate; pterygoids without teeth or nearly so, touching each other anteriorly;

palatal notch not reaching to level of centers of eyes; teeth conical; nostril in a single nasal; frontonasal single or divided; lower eyelid scaly without disc, tympanum large superficial; no supranasals; prefrontals, frontoparietals and an interparietal present. Limbs normal, pentadactyl with transverse lamellae on under surface of digits. (Frontal may be broken into smaller scales.)

Thailand has five forms here recognized as species. Most species are semiaquatic, being found along streams in hills and mountains. They feed largely on aquatic life. *Tropidophorus thai* may be an exception. This form described by Dr. Malcolm Smith in 1919, was still known from three specimens in 1935. I have found only a single specimen and have one other discovered by Mr. Oliver Gordon Young, and presented to me. These two specimens were taken in the forest foraging at one or two hundred meters from streams or other permanent water. Dr. Smith concluded that the species were all mutually exclusive and no two of them occurred in the same areas. My experience has been different. In Mindanao three species have been taken together, and in Thailand, the forms here recognized as *berdmorei* and *thai* have been taken on Doi Suthep, Chiang Mai in northern Thailand within one hundred meters of one another.

A favorite habitat of the species of *Tropidophorus* is in small streams and rivulets especially where an abundance of small rocks offer shelter and hunting grounds. They dive in the water and search under submerged rocks. They also take to the water to elude pursuit.

Tropidophorus berdmorei one of the species found in this habitat on Doi Suthep, is a handsome species, the smoothness of the scales enhancing the contrast of colors especially when their surface is moist.

The genus has a wide distribution in southern China, Assam, Burma, the Philippines, Celebes, and its range reaches to Queensland, Australia.

KEY TO SPECIES OF TROPIDOPHORUS IN THAILAND

1. Three large preanal shields; lateral scales arranged in strongly oblique rows ..... *microlepis*
   Two large preanal shields 2
2. Head scales smooth; dorsal scales with weak keels in adults 3
   Head scales keeled and rugose; dorsal scales strongly keeled 4
3. Frontonasal single ..... *berdmorei*
   Frontonasal divided ..... *laotus*

4. Frontal divided into symmetrical shields; frontonasal divided; the keels on scales directed upwards and backwards ..... *thai*
Frontal not divided; frontonasal single; keels of lateral scales point straight backwards ..... *robinsoni*

The genus, quite surprisingly, has not been reported in Malaya. The southernmost point in Thailand at which specimens have been taken is at Tasan, Chumphon. However, I have seen specimens of a species which I strongly believe to be *Tropidophorus,* once at La Doo Tin Mine, Bendang Stah (Benang Star) under a rock at the edge of a small stream; once 16 km. NE of Bhetong in Yala province where one was dislodged from a small bit of drift against a tree growing in a small stream. Both escaped. Chumphon is 375 kilometers north of these points.

Tropidophorus microlepis Günther

Fig. 76

Tropidophorus microlepis Günther, Proc. Zool. Soc. London, Apr. 23, 1861, p. 188 (type-locality, Chartaboom [= Chanthaburi]); The reptiles of British India, 1864, pp. 76-77, pl. 10, fig. A; M. Smith, Proc. Zool. Soc. London, 1923, p. 781 (Dran, Langbian Plateau, S. Annam); The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 328-329 (Khao Sebab, Chanthaburi).

Tropidophorus cocincinensis: (part.) Boulenger, Catalogue of the lizards in the British Museum (Natural History), vol. 3, 1887, p. 363; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 3, 1919, p. 227.

Diagnosis: Upper head scales rugose or striated; dorsal scales sharply keeled; three enlarged preanal scales; lateral body scales oblique; males with numerous postanal pores.

Description of species (from B. M. No. 1916.6.22.10, ♂. Khao Sebab, Chanthaburi, Thailand): Rostral smooth, thickened considerably, wider than high, forming a curved suture with frontonasal; no supranasals; prefrontals forming a suture half the length of the scales, touching two loreals, one supraciliary, and first supraocular laterally; frontal slightly narrower than widest supraocular, longer than its distance to tip of snout, slightly shorter than combined parietals; frontoparietals larger than prefrontals; interparietal narrow, enclosed behind by parietals; nostril in a single nasal; a small postnasal; two loreals, anterior the smaller; a series of small scales between loreals and supralabials; two presuboculars; seven supraciliaries, the series interrupted by fourth supraocular; lower eyelid with two large opaque scales and some much smaller ones; seven supralabials, first smooth, others at least partially rugose or striate; subocular supralabial largest with a diagonal groove; three

to four rows of temporals, all keeled; two large secondary temporals, bordering parietals posteriorly; labial border of mental greater than that of rostral; six infralabials; an azygos postmental, followed by two pairs of chinshields broadly in contact, and a third pair separated from each other by a single scale; scalerows about middle

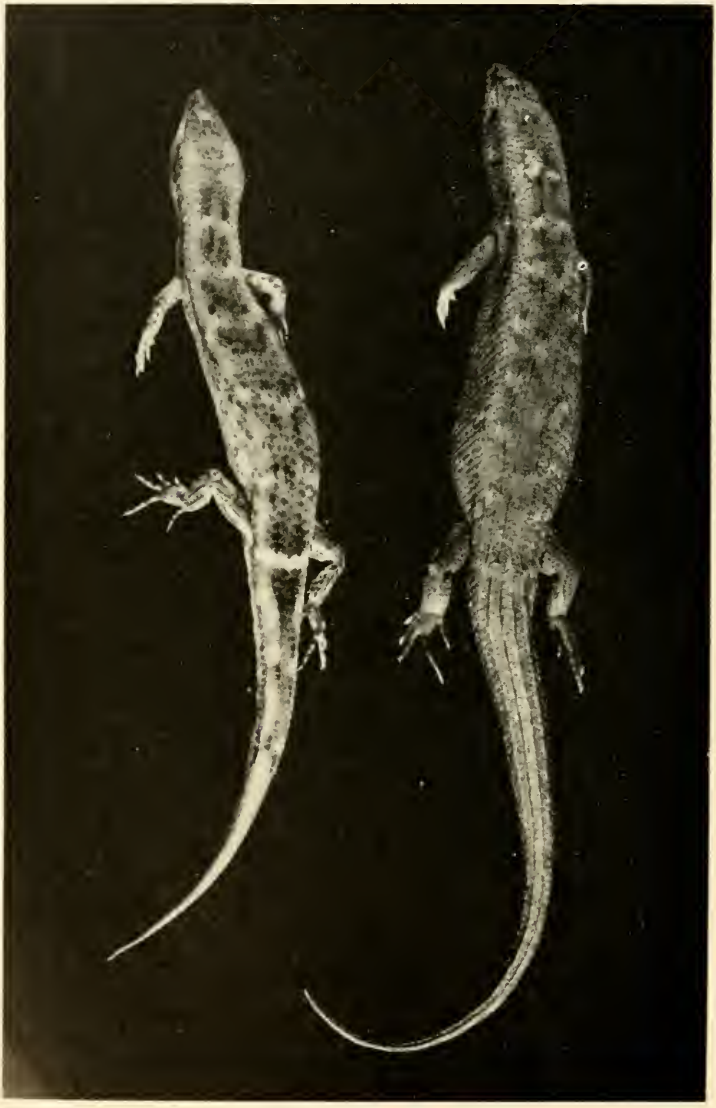


FIG. 76.—*Tropidophorus microlepis* Günther. Left, B. M. No. 1916.6.22.10♂. Actual length 150 mm. Right, B. M. 1921.4.1.142, actual total length, 191. Both from Khao Sebab, Chanthaburi province.

of body, 31; three enlarged preanals; subcaudals beyond base of tail distinctly widened; ventrals smooth as are scales under chin; scales on throat keeled; terminal half of tail regenerated.

Limbs pentadactyl, when adpressed, longest toe reaches wrist; third and fourth fingers subequal with 13 smooth lamellae below; 20 under fourth (longest) toe. Eye moderate; tympanum superficial, its diameter much less than length of eye; a series of about 19 postanal pores, bordering edge of vent in a continuous series.

Color: Ground color of body light brown with six darker dorsal body blotches, the most distinctive intervening light band on dorsum above vent; anteriorly a suggestion of a dorsolateral line below which are some indefinite black spots or fine diagonal black lines; black indefinite line on latter part of body and base of tail; arms with black flecks; fingers and toes banded with black and amber; a light black-edged indefinite stripe on posterior side of leg.

Measurements in mm. (of B. M. Nos. 1916.6.22.10 and 1921.4.1.-142, respectively): Snout to vent, 76, 83; tail (regenerated), 74, 108; tip of snout to arm-insertion, 28.3, 25; axilla to groin, 38, 43; head width, 12, 12; head length, 20, 19; arm, 20.5, 20; leg, 28, 27.

Variation: The second specimen at hand, differs in being a rusty brown with very indefinite dark blotches above separated by lighter areas or bands, and several scattered small lateral rounded light spots; nine or ten ventral scalerows yellow-ivory, the scales narrowly edged with brown. The supracaudal region is nearly uniform dark brown with indefinite ventrolateral lighter spots. At the base of the subcaudal region there are four paired scales, followed by a median row of 85 widened scales, while the five subterminal scales are paired, the terminal one single.

The specimen is a female and the postanal pores are present, but very much smaller than in the male. The keels of the four median dorsal scalerows on the tail form strong continuous ridges.

The specimen contains several eggs.

Distribution: The present known distribution of this species is in southeastern Thailand, in the immediate vicinity of the type locality, Khao (mountain or hill) Sebab, Chanthaburi, and on the Langbian Plateau in South Annam, from which place Dr. Malcolm Smith collected the species.

Remarks: Dr. Smith kept alive two female specimens from the type-locality. At the end of April they produced seven and nine young, respectively. The lengths of the young at birth were 56 and 60 mm., respectively.

In color they were light brown above with indistinct darker markings; the sides were blackish with small white spots. The venter was whitish, the throat mottled with gray.

Tropidophorus berdmorei (Blyth)

FIG. 77

Aspris berdmorei Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 651 (type-locality, Mergui).

Tropidophorus berdmorei: Theobald, Descriptive catalogue of the reptiles of British India, 1876, p. 48; Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 362; Ann. Mus. Civ. Genova, ser. 2, vol. 5, 1887, p. 480; Fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 217; Anderson, Anatomical and Zoological Researches and Zoological Results of the Yunnan Expeditions, Reptilia and Amphibia, 1878, p. 796, pl. 76, fig. 3; Rec. Ind. Mus. 1912, vol. 8, p. 59; Smith, Journ. Nat. Hist. Soc. Siam, 1919, vol. 3, p. 225; Proc. Zool. Soc. London, 1923, p. 776; Fauna of British India, including Ceylon and Burma: Reptilia and Amphibia, vol. II, Sauria Feb. 7, 1935, p. 325 (Mergui, central Tennasserim; north Siam, Pegu, Bhamo, and Yunnan).

Tropidophorus yunnanensis Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 362 (type-locality, Hotha Valley, Yunnan); Fauna of British India, including Ceylon and Burma, Reptilia and Batrachia, 1890, p. 217; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 321; Smith, Journ. Nat. Hist. Soc. Siam, vol. 3, 1919, p. 224.

Diagnosis: No supranasals; scales smooth or posteriorly obtusely keeled; two loreals; six supralabials; two large preanals; prefrontals separated above with dark-edged cream spots; salmon-pink on venter.

Description of species (from No. 33691, Doi Sutep [near Chieng Mai, Thailand], 3000 ft. elevation): Rostral wider than high forming a curving suture with the frontonasal; latter in contact with the frontal thus separating the two small prefrontals; frontal seven-sided, in length, nearly double its distance from tip of snout; frontoparietals two, small; parietals diagonal enclosing small interparietal; four supraoculars the anterior elongate, pointed somewhat, anteriorly touching prefrontal (a small fragment segmented from this scale on each side—abnormal); nostril in a single nasal followed by two loreals; eight supraciliaries, the series interrupted by the fourth supraocular; two presuboculars; six supralabials, first touching first loreal, second both loreals, fourth below eye; a groove from behind nostril crosses fourth labial and terminates at lip; lower eyelid with three or four transparent quadrangular scales separated from supralabials by two or three rows of small granules; two large temporals border parietals; two pairs of nuchals (the second one on left divided); three series of small temporals above last labial; mental large, its labial border nearly double that of rostral; infralabials 5-7, second largest (normally); a large postmental; first chinshields in

FIG. 77.—*Tropidophorus berdmorei* (Blyth) Left figure No. 35908♀. Actual snout-vent length, 82 mm.; tail, regen. 81 mm. Middle figure No. 35960♂. Actual snout-vent length, 74 mm., tail complete, 104 mm. Right figure No. 33691♂. Actual snout vent, 85 mm., tail 101. All from Doi Suthep, *circa* 1000 m. Chiang Mai province, Thailand.

contact; second pair separated by a small scale; third pair small separated from labials.

Head scales not keeled or rugose; dorsal lateral and ventral scales smooth except posteriorly and on tail where they are very obtusely keeled; lateral scalerows run straight forward anteriorly, directed somewhat upwards posteriorly; ventrals largest; two much enlarged preanals each flanked by a smaller scale; median subcaudals larger than adjoining scales; 36 scalerows around middle of body; 64 scales from parietals to above vent; 53 from chinshields to vent; tail somewhat compressed (and regenerated on its terminal portion).

Tympanum large, superficial. Limbs short, the adpressed limbs barely touch; digits below with smooth transverse lamellae, 22 under longest toe; scales on forearm and tibia more or less keeled.

Color in life: Above a rich brown, darker on sides; back and tail with irregular lighter cream spots surrounded by a black area or indefinite dark spots without cream areas; sides of body and tail with very numerous blue-white (often dark-edged) flecks scattered or arranged in irregular vertical rows; upper and lower labials, and chin with more or less continuous rows of light dots; throat ivory with considerable dark pigmentation; venter salmon-pink; tail yellow, below blackish flecked with ivory; some salmon-pink on underside of limbs.

Measurements in mm. of *Tropidophorus berdmorei*

NUMBERS	33691	33695	33693	33689	33687	33688
Snout to vent	85	84	84	81	79	68
Tail	101*	.....	56*	.....	104	83
Snout to arm	28	30	29	30	27	26
Axilla to groin	46	43	42	40	42	32
Head width	11.5	14	14	11.9	10	9.8
Head to front of tympanum	15.5	17	18	17	15	15
Arm	19	21	20	19	18	17
Leg	27.5	30	30	28	27.2	26
Scalerows at middle	36	36	36	36	36	36

* Regenerated.

Variation: The series shows only a moderate amount of variation. One specimen, in eleven at hand, has the prefrontals in contact. All the specimens have 36 scalerows around the middle of the body except one, with 38 rows. Females have narrower heads, and a somewhat longer axilla-to-groin distance in proportion to snout-vent length.

The young specimens (smallest 41 mm. snout to vent) have the scales strongly keeled except on venter and subcaudal region; scales on underside of neck are obtusely keeled or smooth.

Seven specimens have the third chinshields touching the labials on one or both sides and this is probably the normal condition to be expected.

Only two have the tails complete or nearly so, the number of subcaudals being 65 and 62. While the loreals vary in shape the first is not divided. One specimen has the second loreal fused with a presubocular; six specimens have a single nuchal, five have two (or the second present on one side).

Most specimens reported from south of Phrae have the prefrontals in contact, while part have a small separate shield separating them. In the specimens from Me Wang none has the prefrontals in contact. There are two anterior loreals in all specimens from south of Phrae.

Remarks: The species is largely aquatic, all my specimens taken were found in a small mountain stream on Doi Suthep either between rocks or under rocks that were partly in the water or with water close to the sandy surface under them. They feed on aquatic life, chiefly water insects, small crustaceans and worms. When disturbed they disappear under the water or into crab holes that are under rocks.

One female contains 12 ovarian eggs about 6 mm. in length. The species is ovoviviparous.

Distribution: Malcolm Smith reports specimens from Khao Pheung and Pan Ton Pheung in hills south of Phrae; Me Wang district as far north as Pa Meang (800-2000 ft. elevation). (These specimens had 32-36 scalerows, 34 being the most frequent number.) The following specimens were reported as *Tropidophorus yunnanensis* (1919) and later placed with *berdmorei:* Doi Nga Chang, southern Me Wang district, 2000 to 3000 ft. elev.; Doi Sutep (Mt.), Chieng Mai at 1500 ft. elev.

Tropidophorus laotus M. Smith

FIG. 78

Tropidophorus laotus M. Smith, Proc. Zool. Soc. London, Dec. 1923, pp. 777-778 (type-locality, Muang Liep, North of Pak Lai, Upper Mekong, French Laos); The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 325-326.

Diagnosis: Related to *Tropidophorus berdmorei* but differs in having the frontonasal divided, and in having the scales following vent strongly widened; three pairs of nuchals are present, and 36 scalerows.

Description of species (No. 34964 Phu Kading plateau, elevation 3800 ft. Collected by M. R. Pootipong Nupartpat): Head scales smooth with a rather deep groove between frontal and supraoculars; rostral broader than high; frontonasal divided by a longitudinal suture, each much longer than wide; prefrontals in contact broadly; nostril in a single nasal; frontal elongate, narrowed much posteriorly, much longer than its distance to end of snout, slightly longer than its distance to first nuchal; frontoparietal divided (that on right abnormally divided transversely); parietals broadly in contact behind interparietal; three pairs of nuchals; anterior loreal triangular, separated from supralabials; second loreal diagonal, broadly in contact with nasal and second labial; two presuboculars; eight or nine supraciliaries the series interrupted by fourth supraocular; four supraoculars, anterior touching prefrontal, first two touching frontal; two large temporals bordering parietal; other temporals small in three or four rows of three scales each; eyelid with five or six enlarged opaque scales separated from subocular by two or three small scales or scalerows; tympanum nearly as large as eye-opening; six or seven supralabials, fourth below eye bearing a shallow diagonal groove, a continuation of shallow groove between anterior supralabials and other head scales; six infralabials; a mental with a labial border much larger than that of the rostral; an azygos postmental; two large pairs of chinshields first in contact, second separated by a scale, both touching labials; third pair small, separated from labials, and from each other (by 3 scales).

Scales on body in 36 rows at middle directed backwards, ventral scales much larger than dorsals or laterals; laterals distinctly smaller than dorsals; all scales smooth save for a very indefinite suggestion of keels near base of tail; two or three very broad scutes follow vent (postanals); two large preanals; subcaudals widened; (terminal part of tail regenerated); limbs adpressed, the toes reach wrist or a little beyond; scales on underside of thigh and tibia enlarged, subdigital lamellae smooth, rather flat, about 22 under longest toe.

Color in life: Above somewhat olive-brown with a very irregular series of lighter brown marks margined with black; a dorsolateral series of punctate cream spots and numerous lateral punctate cream or greenish white dots on slightly darker sides of body; arms and legs punctate with light and dark flecks. Tail marked in same manner as body. Chin and throat with longitudinal gray and greenish white marks. Venter and underside of limbs pinkish; anal

FIG. 78.—*Tropidophorus laotus* M. Smith. No. 34964, Phu Kading (Mt.) *circa* 3800 ft., Loei province. Actual total length, 183 mm.

region rose; underside of tail gray growing nearly black under regenerated parts. Head uniform olive-brown above; first five labials with white dots; continuous light lines running under chin.

Measurements in mm.: Snout to vent, 75; regen. tail, 108; total length, 183; snout to ear, 16; snout to arm, 29; axilla to groin, 36; arm, 20.5; leg, 27.8; width of head, 11.3; length of head, 18.4.

Remarks: The species has previously been reported from "Nong Kai on the Mekong" (presumably Nong Khai of Thailand). The specimen at hand was captured on Phu Kading Mt. (plateau) at an elevation of about 3800 ft. by M. L. Pootipong Nupart-pat late at night. This is a southern extension of range of approximately 150 kilometers.

The differences of this specimen from the type as shown by the description are not marked. Dr. Smith does not mention specifically the nuchals (shown in figure of *berdmorei*) but one presumes that *laotus* and *berdmorei* are similar in this since he lists the differences between them. The known variation in scalerows is 30-34. He does not describe in detail the postanal scales. There is no small intercalated scale between the prefrontals. However the prefrontal scales are not symmetrical, and are as if a small scale had attached to that on the left side. Likewise it might appear that the anterior loreal had divided and the lower part attached to the posterior loreal.

Tropidophorus thai Smith

FIGS. 79, 80

Tropidophorus thai M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 3, 1919, p. 226; Proc. Zool. Soc. London, 1923, p. 781 (type-locality, Pa Meang, Me Wang district, North Siam); The fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 328.

Diagnosis: Rostral small followed by a divided frontonasal; prefrontals widely separated by a median azygos scale; this followed by a pair of scales; frontal small, followed by a divided frontoparietal; interparietal separating parietals; two pairs of loreals; two large preanals; four enlarged transverse postanal scales; 34 scalerows around middle of body, scales keeled, the keels forming longitudinal ridges; lateral scales small, the keels directed upwards and caudad. Head scales rugose.

Description of species (from No. 72, collected at about 3,080 ft. on Doi Suthep, at the Forestry Experiment Station): Rostral wider than high, relatively small; frontonasal divided mesially into two

FIG. 79.—*Tropidophorus thai* M. Smith. No. 36644, 2075 m. Doi Pha Kao Tost, south of Doi Intanon, Chiang Mai province. Actual total length, 88 mm.

longitudinal moieties; a median azygos scale separates prefrontals; this followed by a pair of scales and another small median azygos scale; frontal small; four supraoculars, anterior largest, triangular; a pair of frontoparietals; interparietal narrow, separating parietals; nostril in posterior part of a single nasal; superciliaries, 8-9; lower eyelid opaque, scaly; seven supralabials, fourth below eye; mental with a much larger labial border than rostral; an azygos postmental; first chinshields large, broadly in contact mesially; next pair of chinshields separated by a single small scale, the two pairs touching labials; third chinshields separated by three scales and from labials by one or two scales; six infralabials; tympanum superficial, large, separated from eye by 12 scales.

About 34 scalerows around middle of body; two median dorsal scalerows composed of smallest dorsal scales; four rows lying on side of the median, strongly keeled, keels forming a more or less continuous ridge; scales on sides keeled, small, keels directed upward and backward; six ventral scalerows larger than dorsals, smooth; scales on neck keeled, mucronate; dorsal and lateral caudal scales strongly keeled; 63 smooth, subcaudal, scales; two enlarged preanals; four basal subcaudals about three times as wide as long.

Arms and legs pentadactyl, well developed, when limbs are adpressed along sides toes in contact with fingers; eleven broad flat lamellae under two longest fingers; 17 similar lamellae under fourth toe; palms and soles covered with flat tubercles.

Color in life: Head blackish above and on sides, with a pink spot on frontal area; labials black with small white marks tending to form continuous white lines under chin; scales on chin and throat darker brown with numerous milk-white flakes. Dorsum variegated pink and rusty brown on sides with dim V-shaped marks bordered by slightly darker marks, more evident on tail; ventral scales show light brown edges and salmon centers; sides brownish with a few dim lighter flecks; sides of tail pink and black with some indefinite spots; subcaudal area blackish with irregular markings of yellow.

Measurements in mm. of Nos. 72 and 36644: Snout to vent, 74, 39; tails complete, 79, 49; snout to arm insertion, 26, 15.5; axilla to groin, 38, 18; width of head, 11, 6.7; head length, 15.5, 10; arm, 16, 10; leg, 24, 14.

Variation: So far as I know only five specimens of this species have been taken. These vary as follows: scalerows about body, 34-38; the scales of the region behind the frontonasal usually show two prefrontals separated by an azygos scale. The front part of

FIG. 80—*Tropidophorus thai* M. Smith, No. 72, elev. *circa* 950 m. Doi Suthep, Chiang Mai province. Actual total length, 153 mm.

the frontal may be broken into two pieces (type) or four or five pieces (paratype No. 3106). The parietals may be separated or form a suture behind the interparietal. The limbs touch or barely fail to meet when adpressed.

A second specimen measured is from the collection of O. Gordon Young. It is dark lavender, the V-shaped light marks are discernible on back and tail. The adpressed leg reaches to the elbow of adpressed arm (legs are normally proportionally longer in young animals than in adults especially old adults).

Distribution: The type locality is Pa Meang, Me Wang, Chiang Mai province, where three specimens were taken. The specimen described here (No. 72) is from an elevation of circa 3,080 ft. on Doi Suthep, Chiang Mai. The specimen was taken about 400 meters from a small stream, foraging under leaves.

The second specimen (EHT-HMS No. 36644), collected by Gordon Young, was found on dry ground under a log, 500 yards from a stream, at 6,800 feet elevation at Doi * Pha Kao Tost, south of Doi Intanon, Chiang Mai.

Tropidophorus robinsoni M. Smith

FIG. 81

Tropidophorus robinsoni M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 3, pt. 3, Aug. 1919, pp. 223-224 (type-locality, Tasan, Chumporn province, peninsular Thailand); Proc. Zool. Soc. London, 1923, p. 778; The fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, 1935, p. 326; Bull. Raffles Mus., no. 3, Apr. 1930, pp. 29-30, fig. 4.

Diagnosis: Head scales rugose or feebly striate; prefrontals in contact; two loreals anterior not divided; dorsal and lateral scales keeled; a single frontoparietal; frontal not divided; lateral scales directed straight backward; 30-32 scalerows about body.

Description of species (from EHT-HMS No. M.254 Malcolm Smith No. 4216 from Tasan, Prachuap Khiri Khan): Dorsal head scales rugose; head and body relatively slender; rostral wider than high, narrowly visible from above; no supranasals; frontonasal large, single; two large prefrontals in contact; frontal longer than its distance from tip of snout, shorter than its distance from nuchal; a pair of frontoparietals; a long narrow sharply pointed interparietal separating large parietals; latter on left side broken in two; four supraoculars, anterior longest, three touching frontal; seven or eight supraciliaries, series broken by fourth supraocular in contact with edge of eyelid; nostril in a single nasal; two rather large loreals

* Doi = mountain.

FIG. 81.—*Tropidophorus robinsoni* M. Smith. EHT-HMS, No. M 254 (Malcolm Smith No. 4216) Tasan, Prachuap Khiri Khan province, Thailand. Actual total length, 155 mm.

subequal in height; two presuboculars; six supralabials fourth largest, below eye; four rows of small temporal scales, one bordering side of parietal considerably enlarged; two pairs of nuchal scales anterior separated from enlarged temporal by a scale; tympanum large, higher than wide, superficial, its greatest diameter (2.6 mm.) much less than length of eye (4.4 mm.), separated from eye by a distance (5.4 mm.) equal or a little greater than distance between eye and tip of snout; mental large, its labial border nearly double that of rostral; four infralabials; a large azygous postmental, followed by three pairs of chinshields, first pair almost completely in contact, second pair separated by a single scale, but touching; third pair separated by two or three scales.

Dorsal scales keeled, nuchals and one or two following scales with more than a single keel; lateral scales keeled, ventrals show only a trace of keeling; two much-enlarged preanals; dorsal caudal scales keeled at base, lateral rows keeled; more distally lower rows keeled; others smooth; 61 + widened subcaudal scales, extreme tip regenerated; 30 scalerows around body.

Legs rather short, barely meeting or failing to meet when adpressed; 15 smooth lamellae under longest finger, 18 under longest toe.

Color in life: Brownish above with bandlike dark marks most distinct on neck; a series of light spots on dorsolateral line; sides brownish with some darker clouding and a few indistinct light brown flecks or spots; tail indistinctly marked with vertical lighter marks laterally.

Below yellowish white, venter rather uniform, sides of chin and throat speckled with darker; undersides of tail thickly spotted with dark brown, and with darker and lighter flecks.

Measurements in mm.: Snout to vent, 64; tail, 91 +; width of head, 9.3; length of head, 17; snout to arm-insertion, 26; axilla to groin, 37; arm, 14.6; leg, 24.

Variation: The parietals may be completely separated or may form a suture behind the interparietal; the nuchals vary between one and three, one specimen having two on one side, none on the other. The supralabials, at least the first two, may have a small longitudinal ridge or keel; a groove above first two or three supralabials cutting across the fourth labial; scalerows are 30 or 32.

Distribution: Only in the type-locality, Tasan, 25 miles west of Chumphon, is the species known in Thailand.

It has been reported in Burma, specimens from Tavoy being in the Indian Museum.

Remarks: Malcolm Smith gives the following measurement of the type. Total length, 165; snout to vent, 75; tail, 90; head length, 15; head width, 8.5; arm, 16; leg, 25.

The 32 paratypes were all obtained at the type locality. The species is ovoviviparous, four to five young being born to each mother.

Genus Sphenomorphus Fitzinger

Sphenomorphus Fitzinger, Systema Reptilium, 1843, p. 23 (type of genus *Lygosoma melanopogon* Duméril and Bibron).

Diagnosis: Limbs well developed, pentadactyl; no supranasals; prefrontals present, in contact or not; two loreals; frontoparietals and interparietal distinct; scales usually but not always smooth; lower eyelid scaly.

This genus is represented in Thailand by nine species. Most of these have been taken relatively few times so that their distribution within Thailand is not well known.

These are smooth-scaled terrestrial lizards rarely seen unless routed out from a hiding place. It is not known whether they are more active at night than in the day. My own experience suggests that they are not, since in my night collecting I have never seen one moving about unless routed out from under debris or rocks.

The species may be distinguished by the following key:

Key to Thai Species of Sphenomorphus

1. Adpressed limbs barely touch, or fail to touch when adpressed; diminutive skinks less than 40 mm. snout-to-vent length 2
   Adpressed limbs overlap at least length of hand; larger species more than 40 mm. snout to vent 3
2. Subcaudals enlarged; one pair of nuchals; 30 scalerows about middle of body; limbs barely touch when adpressed; snout-to-vent 36 mm., *mimicus*
   Subcaudals not enlarged; no nuchals; 34 scalerows; snout to vent 30 mm., adpressed limbs fail to meet ..... *grandisonae*
3. Scalerows about middle of body not more than 30; two or three pairs of nuchals 4
   Scalerows about middle of body 32 or more; nuchals, one pair or none 5
4. Scalerows, 28; three pairs of nuchals; prefrontals in contact; 64 scales from parietals to above vent; median subcaudals slightly enlarged; snout to vent, 109 mm. ..... *praesignis*
   Scalerows, 22-24, dorsal median rows widest; two or three pairs of nuchals; prefrontals not in contact; snout to vent 80 mm., *stellatus*

5. Rostral flat or concave; scalerows round middle of body, 42-44 (rarely 38?); 128 widened subcaudals; rarely a pair of nuchals; 73 scales from parietals to above vent ..... *maculatus*
   Rostral not flat or concave 6
6. No dark lateral stripe; dorsum with small somewhat uniform spots arranged in longitudinal and transverse rows; scalerows, 34-36; a small pair of nuchals or none; dorsal scalerows a little wider than laterals, a few scales following nuchals two to three times as wide as long; snout to vent, 90 mm. ..... *tersus*
   Not so marked; some or most dorsal scales wider than laterals 7
7. Dorsolateral line broken into a series of dark brown spots, each of which may have two prongs on lower sides, and separated from each other by fawn or buff spots; lips and sides of neck spotted brown; scalerows, 34 (35); subcaudals widened; two median scalerows widened somewhat; 74 transverse rows between parietal and point above vent ..... *scotophilus*
   Dorsolateral line normally continuous; large species 8
8. Lateral dark stripe variously flecked and spotted with white; some irregular rows of dark spots on dorsum; scalerows, 38; no nuchals; subcaudals widened; 76 transverse rows from parietals to above vent; snout to vent, 84 mm.; 106 ± subcaudals ..... *lineopunctulatus*
   Lateral stripe black without white flecks or spots; deep black in young often faded and dim (rarely obsolete) in the old; 133 widened subcaudals; a pair of nuchals; scalerows, 34-36; 73 transverse scalerows from parietals to above vent; 97 mm. ..... *indicus indicus*

Sphenomorphus mimicus Taylor

FIG. 82

Sphenomorphus mimicus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 234-236, fig. 9 (type-locality, Dong Paya Fai Mts., N. Siam).

Diagnosis: Small skink, 36 mm. snout to vent; total length 94 mm., prefrontals in contact; no supranasals; three supraoculars touch frontal; no postnasal; two frontoparietals; parietals enclose interparietal; one pair of nuchals; seven supralabials, fifth and sixth enlarged; six infralabials, first small; one pair large preanals. Thirty scalerows about body at middle; ventral scales larger than dorsals; subcaudal scales enlarged. Lower eyelid scaly.

Description of species (from type): Very small skink; rostral about twice as wide as high, forming a curved suture with the frontonasal; latter much wider than long, touching nasal and first loreal laterally; no supranasals; prefrontals forming a broad median suture; frontal longer than its distance from tip of snout, shorter than its distance to nuchals, the sides straight, much narrowed posteriorly; two frontoparietals, larger than interparietal; latter enclosed by large parietals; pair of nuchals (a small scale broken from that on left side); nostril in single nasal; no postnasal;

two loreals second one only little larger and equally as high as first; two superimposed preoculars, lower larger; three small presuboculars, third notching supralabial series; this followed by three small suboculars, the third of which also notches supralabial series; lower eyelid scaled; four large supraoculars, three touching frontal, fourth followed by a small scale that might be interpreted as a

FIG. 82.—*Sphenomorphus mimicus* Taylor. Type. From Taylor, Univ. Kansas Sci. Bull., vol. 43, no. 7, 1962, fig. 9.

fifth supraocular; fifth and six supralabials larger than others, and somewhat elongated; six infralabials, first about half size of second. Buccal border of mental only slightly larger than that of rostral; large undivided postmental; three well-defined pairs of chinshields; first pair in contact, second pair separated by one scale, third pair

by three scales; scales in 30 rows about body, dorsal scales little larger than laterals but smaller than ventral scales; pair of enlarged preanals; subcaudal scales, after tenth, become enlarged, wider and longer than adjoining scales; approximately 61 scales from parietals to a point above vent; 86 subcaudals from vent to tip of tail; when arm and leg are adpressed digits barely touch; third and fourth fingers of equal length, each with eight or nine lamellae; fourth toe longest with 16 lamellae.

Color: Above variegated fawn with clouding or small indefinite spots of brown; a dorsolateral line from snout, broken, or at times continuous and more or less including some small fawn spots most noticeable along shoulder region; line continued along side of tail but growing very indefinite and finally becoming lost; supralabials and infralabials each with a dark brown spot; sides of head reticulated with brown; side of neck and sides with fine flecks of brown; arms and legs strongly spotted with brown and fawn; chin, venter, underside of limbs, and subcaudal region cream-white.

Measurements in mm.: Snout to vent, 36; tail, 58; total length, 94; snout to arm-insertion, 13.2; axilla to groin, 18.4; arm, 8; leg, 13.1.

Remarks: This species, known only from the type-locality, strongly mimics the small leiolopismas in size, color, and form. Nothing is known of the habits of this particular species.

Sphenomorphus grandisonae Taylor

FIG. 83

Sphenomorphus grandisonae Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 236-239, fig. 10 (type-locality "Ban Tong Pheung, M. Siam").

Diagnosis: Small skink; 34 scalerows around body; six supralabials; five infralabials; median suboculars larger than pre- or postsuboculars, the whole series continuous; temporals, 2 + 3 + 4; no nuchals; dorsal scales smaller than ventrals; subcaudals smaller than lateral caudal scales; dorsolateral markings on side reduced; very slight suggestion of brown dorsolaterally on tail; toes fail to touch when limbs are adpressed; third finger distinctly longer than fourth and all fingers relatively short. Seventy-one scales in a line from parietals to above vent.

Description of species (from type): Rostral visible from above, its posterior border convex, forming a suture with frontonasal; frontonasal wider than long; prefrontals moderate, in contact me-

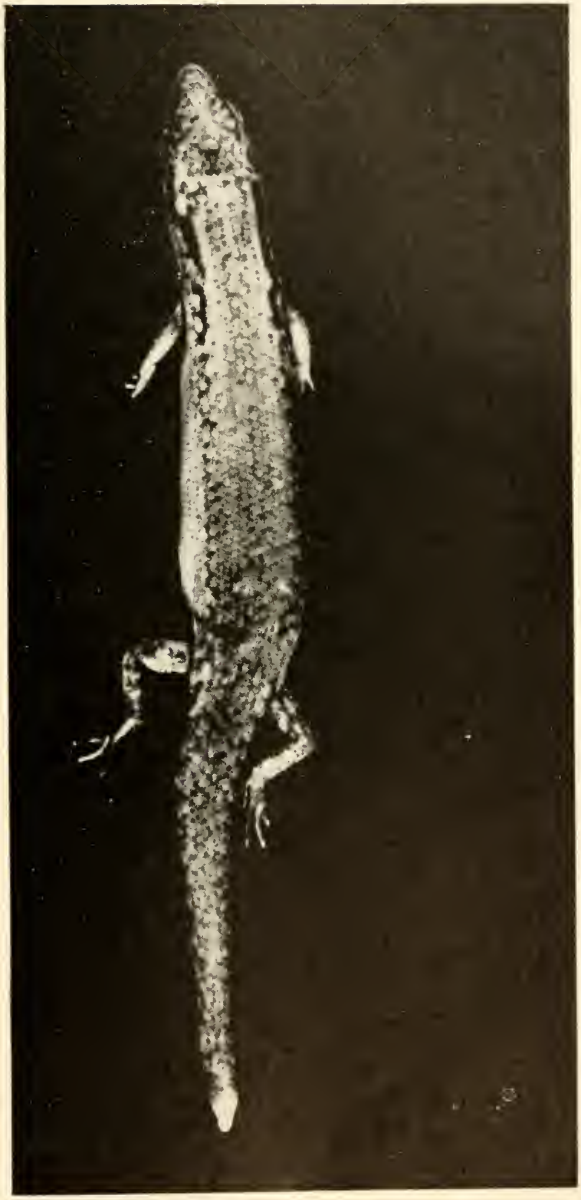


FIG. 83.—*Sphenomorphus grandisoni* Taylor. Type. From Taylor; Univ. Kansas Sci. Bull., vol. 43, no. 7, 1962, fig. 10.

sially, separated from first supraocular; frontal longer than its distance from tip of snout, much shorter than its distance from posterior end of parietal; two frontoparietals, the interparietal enclosed by parietals; no nuchals; nasal diagonally placed, undivided; two loreals, first higher than second; two preoculars; four supraoculars, anterior smallest in area; nine supraciliaries; seven or eight pre-, sub- and postoculars forming a continuous series, none wedged between supralabials; temporals, 2 + 3 + 4; six supralabials, fourth below middle of eye; five infralabials, first largest; mental with a larger labial border than the rostral; a large postmental; three pairs of chinshields touching labials, first pair in contact, second separated by one scale, third by three scales; lower eyelid scaly; tympanum large, superficial; eight scalerows across neck between darker lines; 34 scalerows about middle of body; 24 scales about tail at 14th subcaudal; median subcaudals definitely not larger than adjoining scales, smaller than lateral caudals.

Arm and leg short, the toes and fingers separated when legs are adpressed; median finger distinctly longer than two adjoining digits, with six lamellae; 12 lamellae under fourth toe.

Color: Above light brown with some minute flecking on dorsal scales but no series of spots; head with supraorbital sutures darkened, as are many other head sutures; lips with dark bars on labial sutures, separated by cream spots; a lighter dorsolateral line on side of neck and shoulder; a brown stripe below light stripe, reaching to shoulder but not continued along side except as very indefinite line of scarcely discernible darker flecking with some lighter dots; dark and light indistinct marks on limbs and tail; on chin, venter, and underside of tail, white or cream; tail broken, regeneration begun.

Measurements in mm.: Snout to vent, 30; tail, broken, 21.5; head, width, 4.1; head, length, 8.2; snout to arm, 12; axilla to groin, 16; arm, 6.5; leg, 9.4.

Distribution: Known only from the type-locality.

Remarks: The scales are slightly elevated giving the impression that they are very bluntly keeled. However, they are not keeled. They are arranged in very straight rows, those on the back being of the same size as those on sides, but smaller than most of the ventral scales.

The failure of any of the subocular scales to form a notch between two supralabials and the presence of a large first infralabial equal to second are characters not usually present in *Sphenomorphus.*

Usually the first infralabial is only about half the size of the second.

The species is named for Miss Alice Grandison, Keeper of Reptiles and Amphibians, Department of Zoology, British Museum, who has kindly loaned the specimen for study and description.

Sphenomorphus praesignis (Boulenger)

FIG. 84

Lygosoma praesigne Boulenger, Ann. Mag. Nat. Hist., ser. 7, vol. 6, 1900, p. 191 (type-locality, Larut Hills, 4000 ft., Perak, Malaya); Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 159; Journ. Federated Malay States, vol. 3, 1908, p. 67; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore; Reptilia and Batrachia, 1912, p. 88.

Mabuia praesignc, M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June 1916, p. 55 (Nakhon Si Thammarat); *ibid.*, vol. 2, no. 2, Dec. 1916, p. 156 Khao Wang Hip, upper camp, Nakhon Si Thammarat); Bull. Raffles Mus., no. 3, 1930, p. 31.

Diagnosis: Scales smooth; no supranasals present; lower eyelid scaly; parietals form suture behind interparietal; three pairs of nuchals; auricular opening nearly as large as eye-opening, without lobules; a pair of enlarged preanals; 20 lamellae under fourth toe.

Description of species (from British Museum No. 1906.2.28.15, Gunong Kledang, 2,646 ft. Perak): Rostral about one-fourth wider than high, scale curving back onto snout forming broad contact with frontonasal, nasal and first supralabials; frontonasal a fourth wider than long, touching nasal and first loreal laterally; a pair of prefrontals forming a substantial median suture, in contact with two loreals, first supraciliary, and first supraocular; frontal elongate, a little less than twice as long (7 mm.), as wide (3.7 mm.), the scale very narrow through much of its length; frontoparietals moderately large, forming a median suture, much larger than interparietal which is enclosed by parietals; three pairs of nuchal shields.

Nostril in a single nasal followed by a narrow loreal that is slightly higher than larger one following; two preoculars, lower followed by single differentiated presubocular; four supraoculars, anterior longest, three touching frontal; nine supraciliaries bordering palpebrals; lower eyelid scaly, two median scales somewhat enlarged; three or four small postsuboculars; anterior temporal moderate, separated from parietal by a small (temporal) scale; two large secondary temporals bordered posteriorly by four tertiary temporals, uppermost lying chiefly behind parietal; seven supralabials, fifth being subocular and perhaps largest of series; seven infralabials; mental border on mouth considerably wider than rostral border; an undivided postmental; first chinshields form median suture, second pair separated by a single scale, third pair

FIG. 84.—*Sphenomorphus praesignis* Boulenger. B. M. No. 1096.2.28.15, Gunong Kledang, 800 m. Perak. Actual length, 244 mm.

by three scales; fourth pair small, but like other three pairs in contact with labials, and separated from each other by eight scales.

Auricular opening three millimeters in vertical diameter; tympanum deeply sunk. Snout a little longer than eye.

Scales smooth, two median rows distinctly widened throughout body; approximately 64 from parietal to above vent; 32 scalerows about neck; 28 rows about middle of body; pair of enlarged preanals; median subcaudal scales a little larger than adjoining rows.

Arm moderate, adpressed leg reaching to elbow of adpressed arm; 15 smooth rounding lamellae under longest (fourth) finger; 20 lamellae under fourth toe; latter third of tail regenerated, representing two separate growths on regenerated part.

Color: Above variegated buff-brown to deep brown, with indication of about 16 transverse bands of buff-brown with groups of dark blackish brown dots at sides, and separated by slightly lighter bands, which may have a few whitish scales low on sides; unregenerated part of tail with rather well-defined bands of dark or blackish brown interrupted on ventral surface of tail, separated by narrow bands buff-brown above, grayish on sides; some blackish-brown spots in loreal area. Supralabials with median cream spots separated by dark brown spots on sutures; infralabials similar; less distinct spotting on chinshields; throat, venter, and base of tail immaculate cream to yellow; regenerated part of tail brownish with variegated flecks; scales on arms and legs each with a dark brown fleck or spot; some cream flecks on upper side of leg.

Measurements in mm.: Snout to vent, 109; tail, 135; width of head, 19; length of head, 26; snout-tip to arm-insertion, 41; axilla to groin, 52; arm, 32; leg, 42.

Variation: The type shows some differences from this specimen but agrees in essential points.

Boulenger counts a small scale lying back of the fourth supraocular as a fifth "supraocular." The ear-opening is oval, nearly as large as the eye-opening. There are 28 scalerows, the scales of the two middle rows being twice as broad as long. It is described as "Reddish brown above, with scattered black dots, grey on sides spotted with black and white; a series of large roundish black spots on each side of the neck on anterior part of body; lips spotted with black; tail black above and on the sides with irregular annuli of whitish scales; lower parts white." The total length (in mm.), 240; snout to vent, 110; tail, reproduced, 130; head width, 17; head length, 25; arm, 34; leg, 47.

Distribution: To the best of my knowledge the species is known in Thailand only by specimens obtained at Khao Wang Hip, Nakhon Si Thammarat by Malcolm Smith's collector.

The type locality is in the Larut Hills, Perak, a Malay state bordering Thailand on the south. It is a very rare species in Malaya.

Remarks: Three specimens, two adults and one young one, were collected in Thailand. Smith states that all of his specimens had a small extra shield interposed between the frontals and frontoparietals; the specimen I describe here does not have this anomaly. He states that the parietals are not in contact in one of his specimens. (Smith, Dec. 1916, p. 156.)

Sphenomorphus stellatus (Boulenger)

Lygosoma stellatum Boulenger, Ann. Mag. Nat. Hist., ser. 7, vol. 6, 1900, p. 192 (type-locality, Perak, Malaya); A vertebrate fauna of the Malay Peninsula . . ., Reptilia and Batrachia, 1912, p. 87; M. Smith, Proc. Zool. Soc. London, 1921, p. 431; The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 284-285.

Lygosoma annamiticum Boettger, Senckenbergiana, 1901, p. 47 (type-locality, Phuc-Son, North Annam).

Diagnosis: A species having well-developed limbs; when adpressed leg reaches wrist or elbow; median dorsal scalerows wider than adjoining scales, laterals smallest; two or three pairs of nuchals; 22-24 scalerows around middle of body; a pair of much-enlarged preanal plates; a median and two lateral series of black spots more or less contiguous, interspersed with small starlike light spots.

Description of species (from No. 35439 ♂, Khao Sebab, near Chanthaburi, Chanthaburi province): Rostral moderately large, convex, forming a straight suture with frontonasals; no supranasals; frontonasal wider than long, touching first loreal laterally; prefrontals moderately large separated from each other by a small fragmented portion of posterior margin of frontonasal which prevents contact of latter with frontal; latter much longer than its distance from tip of snout, about as long as combined length of parietals; nuchals, 2-3; nostril in a single nasal; two loreals, anterior a little higher than long; second longer than high; eight supraciliaries; four supraoculars, subequal in size; three temporals, upper secondary very large; seven supralabials; seven or eight small infralabials; mental with a much larger labial border than rostral; a large azygos postmental; three pairs of large chinshields touching infralabials, first in contact, second separated by a scale, third separated by three

scales; a pair of enlarged preanals. Twenty-four scales around neck in a transverse row; 22 scalerows around middle of body; two median dorsal rows widest; those adjoining these also widened; all scales smooth; a few rows of scales preceding preanals are largest ventral scales; subcaudal scales, 62, those immediately following vent transversely widened and largest; terminal part of tail regenerated, scales much widened on regenerated part. Arm and leg well developed, leg reaching wrist of adpressed arm; thirteen scales under longest finger; 18 under longest toe, flattened somewhat at base, compressed distally; ear-opening large, slightly smaller than eye; tympanum superficial; no lobules.

Color in life: Greenish to bronze brown, tail lighter than body; four or five scattered black spots on frontal and preceding scales; one each on supraoculars; a large black spot on fronto-, and interparietals, extending on to parietals; irregular black line of spots, many with fine white dots, from parietals to level of leg-insertion, and continued on tail as a series of small black dots; black spots on supralabials, and a series just below infralabials; black irregular line begins behind eye, extends to groin, and continues on sides of tail as a series of dark vertical bars marking segments, and more or less continuous with a series of subcaudal transverse bars on sides; this black stripe usually with two series of small whitish spots (one directly above other tending to break stripe into a series of spots). In this specimen white markings inconspicuous. Venter greenish white, becoming dark in fixative.

Measurements in mm.: Snout to vent, 57; tail, distal portion regenerated, 59; width of head, 8.5; length of head, 12; snout to arm, 22; axilla to groin, 33; arm, 16; leg, 20.

Variation: There are certain differences indicated between this specimen and the one described by M. Smith (1935). There are two less scales around the middle of body and there are four or five fewer lamellae under the fourth toe.

Distribution: The species has been taken in Thailand at Khao Sebab, Chanthaburi. This is the first and only record for this country. Originally described from the Larut Hills in Perak, it has since been found in southern Annam on the Langbian Plateau.

Remarks: The species was taken by me on the summit of Khao Sebab from underneath dead bark on a standing tree. Another specimen was seen at the same place but it escaped.

Sphenomorphus maculatus (Blyth)

FIG. 85

Lissonota maculata Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 653 (type-locality, Assam).

Hinulia maculata: Theobald, Catalogue of Reptiles in the Museum of the Asiatic Society; Journ. Asiat. Soc. Bengal (extra number) 1868, p. 25; Stoliczka, Journ. Asiat. Soc. Bengal, vol. 39, 1870, p. 174; *ibid.*, vol. 41, 1872, p. 123.

Lygosoma maculatum: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 242; The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 196; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 319; Anderson, Journ. Linn. Soc., vol. 21, 1889, pp. 334, 344; Boettger, Katalog Reptiles Senckb. Frankfurt, 1893, p. 103; Flower, Proc. Zool. Soc. London, 1899, p. 548; Annandale, Journ. and Proc. Asiat. Soc. Bengal, ser. 2, vol. 1, 1905, p. 144; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 154; Hora, Rec. Ind. Mus., vol. 29, 1927, p. 4; Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, pp. 285-286.

Sphenomorphus maculatus: Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, p. 1958, pp. 1116-1118, fig. 17 (Nakhon Phanom province).

Lygosoma mitanense Annandale, Journ. and Proc. Asiat. Soc. Bengal. ser. 2, vol. 1, 1905, p. 144 (type-locality Meetan, S. Burma).

Diagnosis: A small skink (62 mm.); snout short, obtuse, the rostral flattened or concave on dorsal surface, touching frontonasal; prefrontals separated; parietals enclose interparietal; no nuchals; ear-opening about size of eye; a pair of large preanals; limbs well developed, pentadactyl.

Description of species (from No. 33781 Chiang Mai, Thailand): Rostral large broadly visible above, flattened (often depressed) forming a broad suture with frontonasal; no supranasals; prefrontals somewhat quadrangular, separated, touching two loreals laterally; frontal less than twice as long as wide, equally as long as combined parietals; a pair of nuchals; frontoparietals larger than interparietal; parietals in contact behind interparietal; nostril in a large nasal; two loreals, anterior highest; five supraoculars, three touching frontal; eleven supraciliaries; seven supralabials; five pre- and suboculars, the series interrupted; eyelid with three or four transparent scales; temporals, 3-3; mental with a longer labial border than rostral; seven infralabials; a large postmental touching two infralabials; first chinshields in contact; second pair separated by one scale; third pair small in contact with labials; ear-opening vertically oval, much smaller than eye, without trace of auricular lobules.

Scales on dorsum larger than on sides, all scales smooth, in 44 rows; 73 scales from parietals to above vent; 78 scales from chinshields to vent; 124 widened subcaudals; neck scales transversely widened; two enlarged preanal scales flanked on side by two other smaller scales.

Limbs pentadactyl, well developed, the legs reaching beyond axilla; palm of hand covered with rather large (about 20) tubercular scales; sole with two outer metatarsals covered with a few large tubercular scales, the three inner by numerous strongly imbricating smooth scales; fourth toe with 21 compressed lamellae.

Color in life: Above brownish olive or bronzy, growing lighter on tail; top of head with dark areas above orbits and on parietals; rostral light; two series of small black dots on two median scalerows,

FIG. 85.—*Sphenomorphus maculatus* (Blyth). No. 168, Coffee Camp, Na Bon, Nakhon Si Thammarat, Thailand. About natural size.

continued as a single series on tail and with occasional flecks of golden green. A narrow blackish-brown line from snout to eye passing above ear to groin, widening on side so as to cover four scalerows and to some extent adjoining rows, borders of stripe not discrete, with a series of somewhat rounded spots; a whitish line beginning behind eye and passing through ear borders; a blackish stripe below; this followed by a scalerow with a few dark flecks; arms and legs flecked or reticulated with blackish olive; underside of chin, venter, and tail immaculate yellowish flesh. Sides of tail with a dim olive stripe and an indefinite series of lighter dots above it. Some blackish flecks on labials.

Measurements of *Sphenomorphus maculatus*

NUMBER	33781	33784	33788	33787	34012
Snout to vent	47	50	50	53	48
Tail	94	95	95	90	94
Snout to arm	16	19	19	15.5	19
Axilla to groin	22	24	24	23	22.3
Head width	7.5	8	8	8	8
Head length	12	12	12.2	12	12
Arm	15	14	15.2	15	16
Leg	24	23.5	24	23	26

Variation: A dark spot immediately above the arm-insertion is usually present. One specimen has the dorsal coloration very light brown with the brown stripe on side formed by five narrow, more or less continuous lines, the light spots confined to neck and shoulder region; the light line below is continuous, while low on flanks there is only a faint pigmentation. The specimen is a female. In one specimen the white line is all but obliterated, the white dots on the stripe more numerous and smaller.

The number of scalerows around the body varies between 42 and 44 (Smith reports 38-42 variation in its range). The two enlarged scales behind parietals are often broken in which case there are no nuchals and this is the more common condition.

Distribution: The species occurs in Northern India, Assam Yunnan, Burma, Cambodia, and in Thailand as far south as the Isthmus of Kra. It is known in Thailand from the provinces of Sakon Nakhon, Nakhon Phanom, Chanthaburi, Nakhon Nayok, Chiang Mai (Doi Suthep), Kanchanaburi, Chumphon, Trad, and Nakhon Si Thammarat. It has also been taken on the islands of Koh Kut,

Koh Chang, and Koh Mak in the Gulf of Siam. The measured specimens are from Chiang Mai.

Sphenomorphus tersus (M. Smith)

FIG. 86

Lygosoma tersum M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June, 1916, p. 44, pl., fig. 1 (type-locality, Khao Wang Hip, altitude circa 1000 ft., Nakhon Si Thammarat); Bull. Raffles Mus., no. 3, Apr. 1930, p. 34 (Tasan, Pak Chan Estuary, Isthmus of Kra, Chumphon province); The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, p. 284 (Tasan, Chumphon).

Diagnosis: Limbs well developed, pentadactyl; ear-opening distinct; lower eyelid scaly; no supranasals; adpressed limbs overlap; leg does not reach axilla; four supraoculars; 34 to 36 scalerows round body at middle; no lateral dark band; back with small spots arranged in longitudinal and transverse rows, sometimes rather indistinct.

Description of species (from EHT-HMS No. M.251, M. Smith No. 4427 Tasan): Rostral large, the part visible above convex, more than half width of frontonasal, and broadly in contact with it; no supranasals; frontonasal broader than long, touching nasal and loreal laterally; prefrontals rather large, barely touching; frontal elongate, its length nearly double its distance from tip of snout, minutely less than its distance to nuchal; four supraoculars, first largest, two touching frontal; frontoparietals much larger than interparietal; parietals much wider than long, forming a median suture behind interparietal; a pair of small nuchals, the scales following widened, several two to three times as wide (transversely) as long; nostril diagonally placed in rectangular nasal; first loreal rectangular, followed by two larger loreals; two presuboculars; seven supraciliaries, fifth and sixth extremely narrow, in direct contact with palpebral scales; seven supralabials, sixth largest, fifth and sixth below eye; two anterior temporals, two secondaries, upper largest; three tertiary temporals, vertically elongate; lower eyelid covered with several opaque scales; diameter of ear-opening, (2.5 mm.) one half of the length of eye-opening (4.95 mm.); labial border of mental greater than that of rostral; an undivided postmental followed by a pair of large chinshields broadly in contact; second pair following separated by a single scale; third pair separated by four scales, all touching infralabials; seven infralabials.

Scales smooth in 36 rows about middle of body, dorsal scales a little the larger; two median preanal scales much enlarged, scales

FIG. 86.—*Sphenomorphus tersus* M. Smith. EHT-HMS No. 3899, Forest Experiment Station, Khao Chong, Trang province, Thailand. Approximately natural size.

lateral to them much smaller; eight scalerows behind vent, subcaudal scales become widened (tail reproduced and part missing); when limbs are adpressed toes reach to wrist or a little beyond; about 22 flat scales on palm; fingers with flat smooth lamellae, eleven under two longest fingers; lamellae under toes similar to those on fingers, 18 or 19 under longest toe.

Color in preservative: Rather dark brown above, with a black area above each eye; a dark area on parietals; back with numerous transverse bands of dots which begin low on sides but become less distinct or absent posteriorly; these likewise tend to form longitudinal rows; sutures of supralabials marked fore and aft with dark brown to blackish vertical marks.

Measurements in mm.: Snout to vent, 90.5; tail, broken; head width, 12; head length, 20; snout to arm-insertion, 32.5; axilla to groin, 47; arm, 23; leg, 38. The type measures 92 snout to vent; the tail, 170.

Variation: The distance from snout to arm-insertion is contained in the axilla-to-groin distance, 1.45 times, as compared with 1.25 times in the type. The leg reaches forward to a point above wrist, but not to the elbow; the type has 36 scalerows about the middle of the body.

Distribution: The species is known only from Thailand where it has been found in two places: The type-locality, Khao Wang Hip, Nakhon Si Thammarat, and at Tasan, Pak Chan Estuary, Chumphon.

Sphenomorphus scotophilus Boulenger

Fig. 87

Lygosoma scotophilum Boulenger, Journ. Bombay Nat. Hist. Soc., vol. 13, 1900, p. 335 (type-locality, Batu Caves, Selangor, Malaya); A vertebrate fauna of the Malay Peninsula . . . 1912, pp. 88-89; Journ. Federated Malay States Mus., vol. 8, 1920, p. 289 (Sumatra); M. Smith, Bull. Raffles Mus., no. 3, Apr. 1930, p. 34 (Pulau Tioman, Sumatra).

Lygosoma floweri Laidlaw, Proc. Zool. Soc. London, 1901, p. 310 (type-locality, Gunong Inas, Perak).

Diagnosis: Four (five) supraoculars; no supranasals; lower eyelid scaly; limbs well developed; leg reaching between elbow and axilla; when limbs are adpressed; frontal distinctly shorter than combined parietals, not especially narrowed posteriorly; no nuchals; 34 scales about body; subcaudals widened.

Description of species (U.S.N.M. No. 24031, Trang, Thailand): Rostral large, well visible above, forming a rather narrow curved suture with frontonasal; no supranasals; frontonasal much wider

than long, laterally in contact with anterior loreal and nasal; not or barely touching frontal; prefrontals barely touching or not, touching both loreals; frontal in contact with three supraoculars, longer than its distance from tip of snout, distinctly shorter than combined interparietal and frontoparietals; frontoparietals a little longer than

FIG. 87.—*Sphenomorphus scotophilus* Boulenger. USNM No. 24031, Trang province, Thailand. Actual snout-vent length, 35 mm.

wide, posterior borders curving; interparietal narrowly enclosed by parietals which are almost separated posteriorly by a small intercalated scale; no nuchal scales; nostril pierced in a rather large diagonal nasal; no postnasal; first loreal slightly higher but not as wide as second; two preoculars, lower larger than either loreal; two presuboculars; lower eyelid scaly; ear large, smaller than eye, tympanum not deeply sunk, no lobules; two small anterior temporals, two large secondaries, and three or four tertiary temporals; eight supralabials, first small, fifth and sixth largest below eye; nine supraciliaries in a row bordering supraoculars; two or three scales between these and palpebrals anteriorly; eight infralabials; labial border of mental equal or slightly greater than labial border of rostral; a large undivided postmental. Three pairs of chinshields, all touching infralabials, first pair in contact, second pair separated by one scale, third separated by three scales. Seventy-four scales in a row between parietals and a point above vent; median pair of scalerows wider than adjoining scales on anterior half of body; 34 (35) scalerows about middle of body; preanal scales rather feebly enlarged; first eight or ten subcaudals not enlarged, subsequent scales of median row transversely enlarged; terminal portion of tail broken and regeneration begun.

Limbs well developed; third and fourth fingers subequal, with 12 or 13 subdigital lamellae; 19 lamellae under fourth toe; limbs adpressed, leg reaches to a point on arm midway between elbow and insertion of arm; six scalerows on nuchal region widened.

Color: Olive to olive-buff; frontal area rather light; supraoculars and parietal scales with spots or dark lines on scale borders; dorsum brownish fawn with a series of rather heavy dark brown dorsolateral spots which may have two prongs on lower sides, separated by areas of light fawn; legs and arms brownish with fine lighter dots or marks suggesting a reticulum; venter and subcaudal areas light, whitish or yellowish (discolored in preservative), lips and sides of neck spotted brown.

Measurements in mm.: Snout to vent, 35; tail broken; snout tip to arm-insertion, 13.8; axilla to groin, 16; width of head, 6.7; length of head, 11.5; arm, 10; leg, 15.2.

Remarks: I am, at least temporarily, referring this specimen to *Sphenomorphus scotophilus* Boulenger. There are differences of more or less significance. There are four instead of five supraoculars, the frontal is shorter than the combined parietals rather than as long. There are 34 instead of 30-32 scalerows around body; there are 19 rather than 22-23 lamellae under fourth toe.

It will be necessary to compare this specimen with the type of *scotophilus* before the identity of the specimen can be finally confirmed.

Sphenomorphus lineopunctulatus Taylor

FIG. 88

Sphenomorphus lineopunctulatus Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 232-234, fig. 8 (type-locality, Forestry Station, Sanoi River. Ubon province, eastern Thailand).

Diagnosis: Dark olive-brown above with irregular rows of black dots on back; a broad black lateral stripe punctated at intervals with cream dots beginning on shoulder but preceded by one or two separate spots, bordered above by a line of ground color and this in turn by a very narrow (often broken) dotted brownish white line; this stripe bordered below by a broad light line which in turn is bordered below by a dark line from axilla to groin, its lower edge indefinite; no supranasals; frontonasal single; prefrontals separated; no nuchals; eyelid scaly; no postnasal; three pairs of chinshields all touching labials; 38 scalerows around body; ear-opening nearly as large as eye-opening.

Description of species: Rostral large above, not quite reaching level of line between nostrils, forming a broad suture with frontonasal; latter wider than long, broadly in contact with frontal, bearing a semicircular groove around its anterior part (may be accidental or abnormal); prefrontals separated; frontal much longer than its distance from end of snout, slightly longer than combined parietals; frontoparietal divided; interparietal small, enclosed by parietals; nostril in rather large single nasal; two loreals, anterior highest and narrowest; large preocular with smaller scale superimposed; two presuboculars, latter partially wedged between fourth and fifth supralabials; ten supraciliaries, first not touching frontal; four large supraoculars, three touching frontal, first touching prefrontal; lower eyelid scaly; seven supralabials, fifth and sixth below eye; two anterior temporal and two larger secondary temporals; ear-opening nearly as large as eye.

Scales in 38 rows around body; 42 scales around narrowest part of neck; 76 scalerows (transverse) from parietals to above vent; no nuchals; scales on six median dorsal rows transversely widened, especially so on neck; five paired subcaudals basally followed by a series of 106 single scales (15 regenerated). A pair of enlarged preanals; when limbs are adpressed, toes reach to near elbow, 22 bluntly keeled lamellae under fourth toe; in profile, lamellae forming a strongly serrate row.

FIG. 88.—*Sphenomorphus lineopunctulatus* Taylor. Type. From Taylor, Univ. Kansas Sci. Bull., vol. 43, no. 7, 1962, fig. 8. Actual length, 211 mm.

Color in life: Above generally dark olive-brown with head a little darker than body; small black spots on posterior edge of frontonasal, frontal, frontoparietals, and interparietal, and two spots on posterior edges of supraoculars; black marks on supralabial sutures and on temporals; light marks on loreals; one or two black spots on shoulder in front of and above arm-insertion; a black stripe on side, two and a half to three scales wide continued less distinctly on tail, and bearing series of blue-white punctations; narrow whitish dorsolateral line more or less black-edged above, reaching a point above tympanum; dorsum olive with three indistinct rows of black flecks reduced to single median row of larger spots on base of tail; light grayish-white stripe from above arm to groin, but continued on base of tail as a dim dark-gray stripe; leg and to lesser extent, arm, with darker reticulation enclosing lighter flecks; sides of neck plumbeous gray; chin, throat, and breast dirty-white with occasional flecks of blackish; venter and subcaudal region white.

Measurements in mm.: Snout to vent, 84; tail, 127; snout to eye, 6.7; snout to ear, 15; head length, 19.8; head width, 13; snout to arm-insertion, 27.5; axilla to groin, 45; arm, 22; leg, 34.5.

Remarks: It is not impossible that this species is related to *Sphenomorphus indicus,* however, the characteristics, and especially the color pattern, is such that it must be regarded as a distinct species rather than as a subspecies of *indicus.*

Sphenomorphus indicus (Gray)

Hinulia indica Gray, Ann. Mag. Nat. Hist., ser. 2, vol. 12, 1853, p. 388 (type-locality, Himalayas).

Certain populations of *indicus* vary sufficiently to be regarded as subspecifically distinct. One of these is *Lygosoma zebratum* Boulenger from Mt. Muleyit, in southern Burma (Tenasserim), placed in the synonymy of *indicus* by M. Smith. If not specifically distinct, it should be recognized as a subspecies of *indicus.* It has not been reported from Thailand but the probability is strong that it occurs in the Bilauk Tuang mountain range in the peninsular part of Thailand.

I have referred the northern Thai population to the typical form.

Sphenomorphus indicus indicus (Gray)

FIG. 89

Hinulia indica Gray, Ann. Mag. Nat. Hist., ser. 2, vol. 12, 1853, p. 389 (type-locality, Sikkim [restricted], Himalayas); Stoliczka, Journ. Asiat. Soc. Bengal, vol. 41, 1872, p. 122, pl. 4, fig. 2.

Eumeces indicus: Anderson, Proc. Zool. Soc. London, 1871, p. 158.

Lygosoma indicum: Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 241, pl. 16, fig. 1; The fauna of British India, including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 195; Ann. Mus. Civ. Genova, ser. 2, vol. 13, 1893, p. 319; Wall, Journ. Bombay Nat. Hist. Soc., vol. 18, 1908, p. 505; M. Smith, Bull. Raffles Mus., no. 3, 1930, p. 33; Journ. Nat. Hist. Soc. Siam, vol. 6, 1923, p. 200 (Hainan); Hora, Rec. Ind. Mus., vol. 29, 1927, p. 4.

Sphenomorphus indicus: Schmidt, Copeia, 1928, p. 80; Pope, Bull. Amer. Mus. Nat. Hist., vol. 58, 1929, p. 380.

Sphenomorphus indicus indicus: Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1113-1116, fig. 16 (Loei).

Lygosoma cacharense Annandale, Journ. Asiat. Soc. Bengal, new ser., vol. I, 1905, p. 145 (type-locality, Nemotha, Cachar) (*fide* M. Smith).

Lygosoma bowringi: (*non* Günther) Mell, Arch. für Nat. Berlin, vol. 88, 1922, p. 113 (*part. fide* M. Smith).

Lygosoma indicum indicum: Smith, Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, Feb. 7, 1935, pp. 281-282.

Diagnosis: A large skink (snout to vent, 97 mm.); rostral convex, not depressed above, in contact with frontonasal; prefrontals separated; sole and palm covered with tubercles, brown, with or without some scattered dark spots; dark lateral stripe usually edged with lighter color above. Siam specimens usually with 34-36 scalerows around middle of body; ovoviviparous; limbs well developed, overlapping when adpressed.

Description of species (from No. 33759, Doi Suthep near Chiang Mai, Thailand): Snout short, rostral convex, forming broad suture with frontonasal, which is broader than long; no supranasals; frontal as long as combined parietals, touching three supraoculars; paired frontoparietals little larger than interparietal; parietals inclosing interparietal; pair of nuchals; nostril in single nasal; two loreals, the anterior highest touching two supralabials; posterior also touching two supralabials; three presuboculars, anterior large; nine supraciliaries; four large supraoculars, one large anterior temporal not touching parietal; two large secondary temporals; three tertiary temporals upper bordering parietal; eight supralabials, fifth and sixth below eye; postoculars scarcely differentiated; labial border of mental equal to that of rostral; eight infralabials; large postmental; three pairs of chinshields, first in contact; second pair separated by one scale, third touching labials, small.

Lower eyelid with four or five semitransparent scales and three rows of granules; ear-opening nearly size of eye-opening, vertically oval without lobules on border.

Scales on body smooth, imbricating, subequal, in 34 rows around middle of body; 73 scales in row between parietal and point above vent; 75 scales between first chinshields and preanals; 133 widened

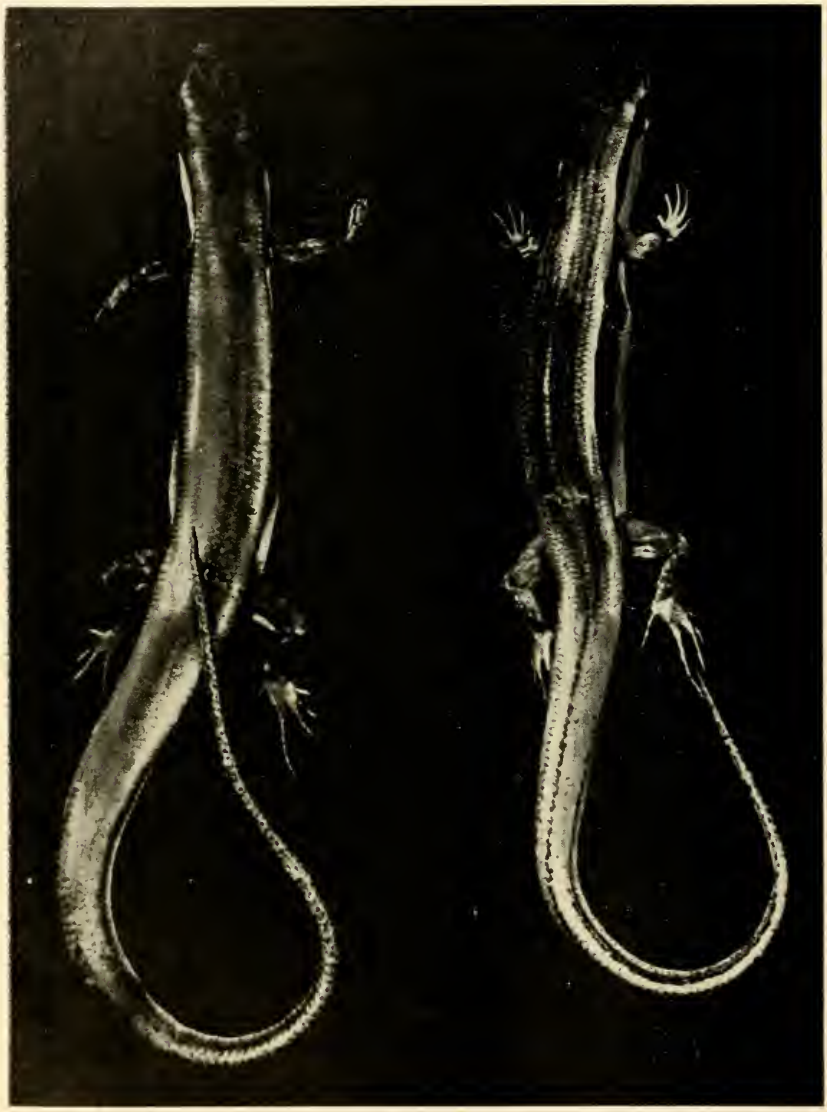


FIG. 89.—*Sphenomorphus indicus indicus* (Gray). Left figure, No. 36128. Actual snout-vent length, 80 mm.; total length 245 mm. Right figure, No. 35913. Actual snout-vent length 74 mm.; total length, 195 mm. Both from *circa* 1000 m. Doi Suthep, Chiang Mai province, Thailand.

subcaudals; pair of large preanals, each bordered laterally by two scales.

Limbs well developed, leg reaching to halfway between wrist and elbow; palm and sole covered with tubercles, those on hand slightly imbricating; 18-19 lamellae under fourth toe. Scales on back of thigh somewhat elongate but not enlarged.

Color: Head brownish or olive-brown, central area of dorsal scales darker; outer scalerows on dorsum lighter than back, bordering the lateral stripe, beginning on snout widening on sides so as to cover most of four scalerows; lower flanks whitish with little or no pigment; chin, venter, and underside of tail immaculate whitish. Tail lighter than body, with median and two dorsolateral lines composed of black flecks continued to tip.

Black markings on back small to microscopic; labials with dim black lines along sutures especially on supralabials. Arms and legs much lighter (nearly fawn-color) with little dark pigment.

Measurements in mm. of *Sphenomorphus indicus indicus*

NUMBER	33759	33761	33762	33758	33760	33763
Snout to vent	81	82	82	92	97	72
Tail	148	154	.....	.....	.....	147
Snout to arm	27.5	27.8	27	30	29.8	24
Axilla to groin	45	43	42	50	53	35
Head width	12	12	14	14.5	13.6	11
Head length	19	19	19.4	21	21	15.6
Arm	23	23	24	24.2	25	20
Leg	34	34	35.2	37.2	36	32

Variation: The problem of subspeciation in this species has not been solved. Evidence points to considerable variation in various populations outside of Thailand. Most of my material is from Northern Thailand, the measured series being from Doi Suthep, Chiang Mai.

The young specimens (snout to vent 45 mm.) have scales strongly striated with (usually) broken sinuous striae, 25 to 30 in number. The color of the dorsum is dark, almost blackish brown. The black lateral line is very distinct, its lower edge somewhat uneven or sinuous. On side of head and neck below the black stripe, it is cream-white to greenish white with two series of spots, one on supralabials and one on infralabials. These continue back on side of head and neck to arm-insertion. Bordering the dorsolateral black

stripe below is a fine ivory-white line, often seemingly broken into spots by the irregular black edge.

Specimens 65 to 72 mm. snout to vent, still display the striations on the scales, usually more pronounced on the posterior part of back and on the flanks. The marks on the neck tend to disappear, but the labial marks are still more or less distinct. There is a more or less distinct hair-fine light line bordering the dorsolateral stripe above, while the line below the stripe is now obsolete.

In the oldest (largest) specimens, those with a dark black lateral stripe may show some darkening on the edges of the dorsal scales, and when submerged in clear liquid seven darker lines may be discerned. A few specimens, regardless of sex, lose the dorsolateral stripe, the region showing a slight olive tinge or a light brown color. The labial spots are missing in old adults. A number of specimens have dotted lines on the tail, the median dorsal line being most distinct.

In squamation the differences are not great. The primary temporal is divided in two about 50% of the time, exactly so in 17 adult specimens; sometimes they are the same on both sides of the head; in five cases it is divided on one side but not on the other. The scalerows in this series of 17 are 32 (3 times), 34 (9 times), 36 (five times).

Distribution: In Thailand the species is known from the northwestern part of the country. Practically all specimens I have taken or seen are from the mountain of Chiang Mai, Loei and Phrae provinces.

Elsewhere it is known in northern India, Sikkim, Assam and Burma and "all of Indo-China" (*fide* Bourret *), southern and central China, occurring as far north as Nanking in the east, Shensi and Szechwan in the west (*fide* Pope **).

Pope ** suggests that valid subspecies occur in China and several have already been defined by other authors.

Remarks: The young of *indicus* are born alive, six to nine young being produced in the same litter.

The species has been reported from Malaya based on certain specimens taken on Fraser's Hill. They may well represent a new subspecific form, and should be re-examined. They may be more closely related to *zebratus* than to *indicus*.

* Bourret, Notes herpétologique sur l'Indochine Française, Anneu Bull. Gen. Inst. Publ. 4 Dec. 1939, p. 52.

** Pope, The reptiles of China, Nat. Hist. Cent. Asia, vol. 10, 1935, p. 482.

Leiolopisma Duméril and Bibron

Leiolopisma Duméril and Bibron, Erpétologie générale . . ., vol. 5, 1839, p. 742 (type *Scincus telfairii*).

Diagnosis: No supranasals; an opaque or transparent disc in lower eyelid; frontoparietal divided or single.

The taxonomy of this group of skinks, a part of the old genus *Lygosoma* (*sensu* Boulenger), has not been very stable. Some ten other genera were proposed before 1879, when Boulenger placed them under *Lygosoma*. While many authors have used this "catch all" others have regarded *Leilopisma*, with its numerous included generic synonyms, a legitimate genus. Mittleman * has attempted to divide *Leiolopisma* into several genera using as generic characters, reduced size of interparietal, size of ear-opening, length of limbs; digit loss, as well as the more conventional criteria. It is not impossible that a better understanding of the skinks will be obtained by a recognition of some of the genera he has proposed or revised, but in its present form Mittleman's paper is in many ways still unsatisfactory. I believe it is a step in the right direction.

These small skinks are difficult to deal with largely because of their small size. If differences are magnified in relation to the whole animal they often seem, as they should, of greater significance. Another fact is that in the Scincidae differences of specific rank may involve fewer scales and as pointed out by Stejneger, may require one to consider more carefully, the scales in the temporal region. I also suggest that pre- and postsuboculars and their relation to the labial series may serve to distinguish groups of species in the Scincidae.

The number of these small species in Thailand is not certainly known, largely because the number of specimens available from any given locality is small, and the amount of variation is unknown. If one accepts the "law of vagility" which states that "small and burrowing forms of reptiles and amphibians, being least vagile, have a tendency to speciate more than larger, more vagile forms," one might expect to find a fair number of species and subspecies in Thailand. They are timid species that seemingly rarely expose themselves to sight, and this would seem to be a habit that serves them for survival.

I have placed ten nominal forms in the key as species or subspecies. Whether *Leiolopisma reevesii* occurs in Thailand is still open to question. I have compared specimens of Dr. Cochran's

* Smithsonian Misc. Coll., vol. 117, no. 17, 1952.

eunice with specimens of *reevesii* from Canton, China (a probable type-locality for *reevesii* in "southern China") and while the Cantonese material has been preserved a much longer time I believe the two are distinct. I suspect that Dr. Malcolm Smith considered *reevesii* a Thai resident because of his opinion that *eunice* and *reevesii* were synonyms. One of the chief distinguishing features between them is size of the subcaudals in *reevesii*.

While I am not completely satisfied with this treatment, because of inadequate materials, the following key is offered as a tentative arrangement of the Thai forms:

KEY TO THAI SPECIES OF LEIOLOPISMA

1. Frontoparietal single; prefrontals broadly in contact; no transversely widened nuchals; a lateral dark line bordered by a light dorsolateral line above; eight scalerows between dark lateral stripes; adpressed limbs overlap about length of hand; 30 scalerows at middle of body ..... *pootipongi*
   Frontoparietal divided 2
2. Body with continuous stripes of black and white (green or gold) 3
   Body lacking continuous black and light stripes 4
3. Five light stripes (white, greenish-white, yellowish or golden) with four black stripes; tail orange; 30-32 scales around middle of body; three pairs of nuchals ..... *vittigerum microcercum*
   A median stripe (white, greenish or golden in life) from tip of snout to tip of tail; sides light brown or greenish, speckled with black; 22-26 lamellae under fourth toe; 28-30 scalerows around middle of body ..... *vittigerum vittigerum*
4. Adpressed limbs fail to meet in adults (may touch in very young) 5
   Adpressed limbs touch or overlap in adults and young 8
5. Nuchals present 6
   Nuchals absent 7
6. Scales in 34 rows around middle of body; adpressed limbs fail to meet by length of foot; "several pairs of feebly enlarged nuchals"; subcaudals somewhat enlarged; 18 lamellae under fourth toe; light gray to cream-white (yellowish white) below ..... *eunice*
   Scales in 28 rows around middle of body; six scalerows on back; three pairs of nuchals; 18 lamellae under fourth toe; limbs narrowly fail to meet; drab gray on undersurfaces ..... *smithi*
7. Scales in 26 rows about middle of body; 14 lamellae on underside of fourth toe; tail nearly twice length of head and body; anterior loreal longer than high. Limbs fail to meet by length of arm; subcaudals not enlarged ..... *tavesae*
   Scales in 30-32 rows around body at middle; 15-17 lamellae under fourth toe; limbs narrowly fail to touch in adults; subcaudals slightly enlarged; brown dots on throat ..... *kohtaoensis*

8. No dark lateral stripes or lateral series of dark spots; snout to vent, 51 mm.; prefrontals touch at a point; scalerows 34; leg reaches to elbow when limbs are adpressed; 20 lamellae under fourth toe; a median pair of nuchals ..... *siamensis*

A dark lateral stripe or lateral series of dark spots 9

9. Adpressed limbs overlap slightly in adults; 36-38 (34) scales about middle of body; lower rows of scales with small black dots, forming broken lines encroaching on venter slightly, and on underside of neck; prefrontals form a good suture; no nuchals; larger, snout to vent, 60 mm.; small scattered dorsal spots ..... *melanostictum*

Adpressed limbs overlap, the leg reaching elbow or beyond; a feebly enlarged pair of nuchals; 30 scalerows about middle of body; snout-to-vent length, 50.5 mm.; a paired series of subquadrangular spots on anterior half of body, united posteriorly ... *rupicolum*

Leiolopisma pootipongi Taylor

Leiolopisma pootipongi Taylor, Univ. Kansas Sci. Bull., vol. 40, 1962, pp. 244-246 (type-locality, Forest Station, Sanoi River, Ubon (province), Thailand).

Diagnosis: A small skink (snout to vent about 38 mm.); frontoparietal single; prefrontals broadly in contact; a dorsolateral light line separated from its fellow by six scalerows; a lateral dark stripe bearing some small white dots; limbs overlap the length of hand; 30 scalerows about middle of body; 66 scales in a line from parietal to above vent.

Description of species (from type): Rostral large, much wider than high, forming a broad suture with frontonasal; frontonasal nearly twice as broad as long touching first loreal laterally; prefrontals large, broadly in contact, laterally touching both loreals and first supraocular; frontal narrowed to a blunt point posteriorly, touching two oculars, a little longer than its distance from tip of snout, shorter than combined length of frontoparietals and parietals; four supraoculars, anterior triangular; eight supraciliaries; nasal single; anterior loreal higher and narrower than second; three presuboculars, third wedged between edges of fourth and fifth supralabials; three or four postsuboculars, last wedged between fifth and sixth labials; seven supralabials fifth and sixth below eye; two small temporals between sixth labial and the very large temporal bordering parietal, one between seventh labial and same scale.

Lower eyelid with an undivided transparent disc; ear opening relatively large (1.2 x 1 mm.); six infralabials, first very small; mental with a larger labial border than rostral; one large azygos post-

mental; first pair of chinshields in contact; second largest, separated by one scale, third by three scales, fourth by four scales, all chinshields in contact with infralabials. Thirty smooth scalerows around middle of body (slightly farther forward the count is 32); eight scalerows on back subequal, except scales following parietals in median rows are somewhat transversely widened; subcaudal scales near base of tail not noticeably enlarged; farther out median scales distinctly wider than adjoining ones; two preanals large; adpressed limbs overlapping; 18 lamellae under fourth toe; 66 scales in a median row between parietals and a point above vent.

Color: Above brown to olive-brown; the supraocular areas of head dark. A pair of dorsolateral light lines, moderately distinct; on middle of back a row of dark spots paired anteriorly; an indefinite dark streak along dorsum of tail with a wide lighter dorsolateral stripe bordered laterally by an indefinite darker line; a dark lateral stripe beginning behind eye, passing distinctly above ear, very irregular on its lower edge, bearing several small punctate light spots; dark color widens on neck and shoulders, reaching down almost to arm-insertion and here bordered by a light line; lower flanks, chin, venter, underside of limbs and subcaudal region immaculate, all whitish except subcaudal region pinkish; labials cream with sutures bordered by darker blackish-brown pigments; arms and legs brownish enclosing lighter spots.

Measurements in mm. (type): Snout to vent, 37.2 tail broken; snout to ear, 7.6; length of head, 9.4; width of head, 5; snout to arm-insertion, 13.7; axilla to groin, 19; arm, 10; leg, 13.8.

Remarks: This species is known only from the type locality and only from the type. It seems that on the basis of the undivided frontoparietal it is related to the Indian *L. palnicum* but differs in the narrower dorsal scales. In *palnicum* the dorsals are three times as wide as long. The species is named for M. R. Pootipong Nupartpat Varavudhi in Chulalongkorn University who accompanied me on numerous journeys into the hinterlands of Thailand.

Leiolopisma vittigerum (Boulenger)

Two subspecies are recognized that may be differentiated by the following key:

A median light stripe, greenish yellow or golden (iridescent), bordered on each side by black stripes; a short dorsolateral dark stripe anteriorly ..... *L. vittigerum vittigerum*

Five light stripes with four well-defined black stripes, *L. vittigerum microcercum*

Leiolopisma vittigerum vittigerum (Boulenger)

Lygosoma vittigerum Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. XIV, 1894, p. 615 (type-locality Sereinu, Mentawei Islands); Journ. Federated Malay States Mus., vol. 3, 1908, p. 67; A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore; Reptilia and Batrachia, 1912, p. 94; Smith, Journ. Nat. Hist. Soc. Siam, vol. 1, 1915, p. 154 (Bong Tee Valley, Sai Yoke); *ibid.*, vol. 2, June, 1916, p. 56.

Lygosoma pulchellum: (*non* Boulenger) Annandale, Journ. and Proc. Asiat. Soc. Bengal, new ser., vol. 1, 1905, p. 145.

Leiolopisma pranensis Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 18, fig. (type-locality Pran, Siam) lat. 12°, 40′ N. (*fide* M. Smith).

Leiolopisma vittigerum vittigerum: Smith, Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 8, fig. 3 (numerous localities).

Diagnosis: A diminutive skink; snout rather pointed; three or four pairs of nuchals; ear-opening smaller than transparent disk on eyelid, without lobules; median pair of dorsal vertebral scales widened; two large preanals; subcaudals widened; prefrontals in contact; median light or golden stripe bordered by black stripes; sides greenish olive, with or without black dots or flecks; ventral surfaces greenish white.

Description of species (from Chanthaburi, B. M. No. 1933.12.1.9): Snout distinctly narrowed, tip rather pointed; rostral large, well-visible above forming a curving suture with frontonasal; latter a little broader than long; *prefrontals very large* broadly in contact; frontal widest at anterior level of supraoculars, much narrowed behind; shorter than its distance from tip of snout, shorter than combined length of parietals and frontoparietals; frontoparietal divided; interparietal biangular a little wider than long enclosed behind by parietals; two pairs of nuchals, first pair longer than second, equally widened transversely; a single nasal; two low, rather elongate loreals; two preoculars; one presubocular; four supraoculars; an elongate primary, two secondary temporals, lower largest, and three tertiary temporals; upper tertiary much enlarged, not widely separated from its fellow. Ten or eleven supraciliaries; eight supralabials, sixth largest, below eye; six or seven infralabials; border of mental on lip larger than that of rostral; an undivided postmental; first pair of chinshields in contact, second pair separated by a scale, third pair separated by three scales.

Scale rows about body 28; four median rows strongly enlarged, two median larger than adjoining rows: 76 + subcaudals (extreme tip of tail missing); leg reaching nearly to elbow when limbs are adpressed; fourth finger longer than third, with 23 lamellae, those on basal two thirds widened, close together, distal ones compressed;

fourth toe longer than third with 29-30 lamellae, all close together, basally compressed, longer distally.

Color: A broad median yellow stripe covering halves of the two median rows of scales, extending from tip of snout to tip of tail; two brown bands bordering yellow line extending onto base of tail, commencing on second supraocular; a narrow yellow line on outer part of supraocular, can be traced to above arm-insertion; a faint darker line below it on occiput and neck; sides with indistinct traces of lines on lateral scalerows; sides of tail pigmented, occasionally showing flecks or small spots distally; underside greenish white, somewhat iridescent on chin.

Measurements in mm.: Snout to vent, 36.5; tail, 40 +; width of head, 5; length of head, 11; snout to arm-insertion, 16; axilla to groin, 19; arm, 10.8; leg, 14.2.

Variation: B. M. No. 1916.6.22.7, Klong Bang Lai, has the sides speckled, the dots scarcely forming rows. The tail is reproduced and there are broad narrow scales above as well as below. There are four nuchals on one side, three on the other; there are three anterior temporals instead of a single one. The ear-opening is much smaller than the palpebral disc. There are seven supralabials, and 28 scalerows.

Distribution: M. Smith reports the species in Thailand from "Tasan, Isthmus of Kra; west of Kanburi [= Kanchanaburi]; Pran; Chantaboon [= Chanthaburi]; Raheng district; Meh Lem, Meh Wang in N. Siam." Outside of Thailand it occurs in Southern Burma, Malaya and the western part of the Indo-Australian Archipelago.

Remarks: This species is arboreal and ranges from sea-level to 1500 m. in the mountains. I have observed occasional specimens at some elevation in trees but they were inaccessible to me, and escaped by going higher or entering cavities. Occasionally the lateral black stripes are reduced, and rarely are absent.

Leiolopisma vittigerum microcercum (Boettger)

FIG. 90

Lygosoma (Leiolopisma) microcercum Boettger, Ber. Senckenb. Naturf. Ges., 1901, p. 49 (type-locality, Phuc-son, North Annam).

Lygosoma vittigerum kronfanum M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 4, 1922, p. 208 (type-locality Daban, Langbian Plateau, South Annam); Schmidt, Copeia No. 168, 1928, p. 80.

Leiolopisma vittigerum microcercum: M. Smith, The Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 308.

Diagnosis: Five light buff dorsal and dorsolateral stripes separated by black stripes; ear-opening very large; 30-32 scales around body; tail orange.

Description of species (from 34933, Sanoi River, Ubon province, Thailand): Snout somewhat pointed, twice as long as eye; rostral wider than high forming a broad straight suture with frontonasal; nostril in a small nasal; frontonasal about as wide as long; prefrontals broadly in contact (that on left side abnormal, partly fused to frontal); frontal relatively small, pointed behind, shorter than its distance from end of snout and distinctly shorter than its distance to first nuchal; frontoparietal divided; interparietal triangular; parietals forming suture behind interparietal; four pairs of nuchals, first pair not touching on mesial line; two loreals, subequal in size but anterior slightly higher, and touching both first and second supralabials; two presuboculars; four supraoculars three touching frontal; seven supralabials, fifth is the subocular, sixth separated from large upper temporal by one temporal scale, seventh labial separated also by one scale; seven supraciliaries; lower eyelid with a transparent disc larger than ear-opening; parietal bordered by two temporals; mental with a labial border larger than that of rostral; an azygos postmental; three pairs of chinshield all touching labials, first pair in contact, second separated by one scale, third by three scales. Dorsal scales, larger than others, especially two median rows; 28 scalerows about middle of body; lateral scales smaller than dorsals or ventrals; pair of very large preanals; subcaudals distinctly widened (tip of tail lost). Arms and legs adpressed, toes reach elbows; subdigital lamellae of proximal phalanges somewhat elevated and widened; seven or eight distal lamellae not modified but compressed, forming indefinite keels.

Color in life: A median greenish golden stripe widening at base of tail, becoming orange in color and continuing to tip of tail; this bordered laterally by two wider black stripes that terminate at base of tail but continue as two lateral rows of small spots to tip of tail; greenish white dorsolateral light lines begin anterior to eye, pass across supraoculars and terminate at base of tail; these bordered below by a dark stripe beginning on tip of snout and extending to base of tail; below this a white line, beginning on labials and extending to groin; below this an indefinite darker line terminating in groin; chin, venter, and underpart of tail lacking dark pigment, the tail rosy beneath, orange above and on sides; the white stripes with some slight admixture of dark pigment.

Measurements in mm.: (Nos. 34933 and 34932, respectively). Snout to vent, 35.2, 36; tail, 34 +, ?; snout to ear, 8.3, 8; snout to arm-insertion, 16.5, 14.4; axilla to groin, 16, 16; arm, 10.5, 11; leg, 11.4, 12; head length, 9.8, 10; head width, 5.8, 5.5.

Distribution: Known from Forest Station, Sanoi River, Ubon, Thailand. Elsewhere it occurs in Viet Nam probably also in Cambodia and southern Laos.

Remarks: Specimens were taken at the base of a tree in second growth forest. Others seen escaped by going high in trees.

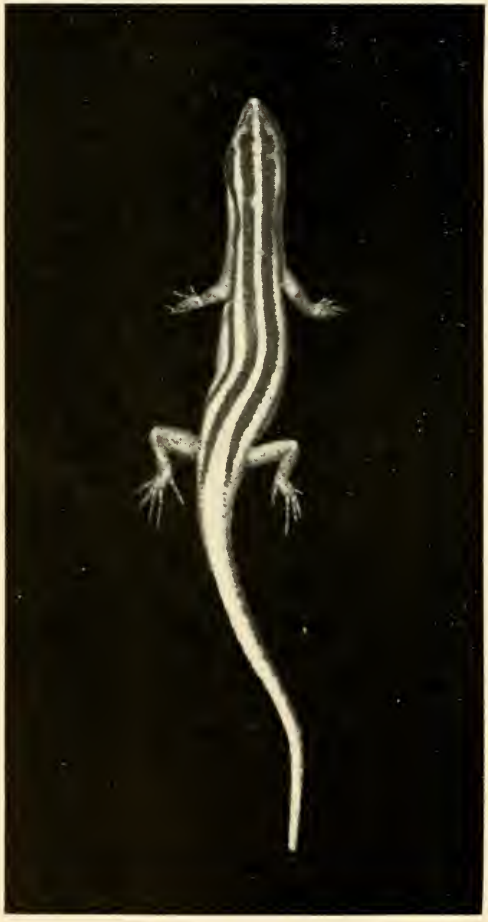


FIG. 90.—*Leiolopisma vittigerum microcercum* Boulenger, No. 34933, Sanoi River Forest Station, Ubon province. Actual snout-vent length, 35.2 mm.

The modification of the subdigital lamellae seems to be an adaptation to climbing.

The type of *microcercum* in the Senckenbergian Museum Frankfurt am Main was examined. The following characters were verified: two pairs of nuchals; two frontoparietals; prefrontal broadly in contact; eye disc large; seven supralabials, fifth directly below eye; interparietal enclosed by parietal; median pair of scales widest; adjoining scalerows also enlarged, and larger than outer bordering rows; 30 scalerows around middle of body; 24 lamellae under fourth toe. The coloration after sixty years of preservation is as follows: a median light bluish green stripe from snout to tail; tail yellowish, two bordering dorsal black lines are lost on tail; the dorsolateral light lines below the black lines begin on eyelids or just in front of them; a lateral brownish stripe begins behind eye and passes above small ear-opening; below this a ventrolateral light stripe, scarcely separable from the whitish ventral coloration; labial sutures with dim brown marks. On sides of proximal half of tail a series of eight rather small diffuse brown spots appear in advance of the regenerated part of tail.

Leiolopisma eunice Cochran

FIG. 91

Leiolopisma eunice Cochran, Proc. Biol. Soc. Washington, vol. 40, Dec. 2, 1927, pp. 187-188 (type-locality, Bang Suk near Pak Jong, Thailand); Proc. U. S. Nat. Mus., vol. 77, 1930, p. 18, fig. 3, Doi Angka, 700 ft.; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, pp. 1121-1122, fig. 19.

Leiolopisma reevesi reevesi: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 295-296.

Diagnosis: Scalerows 32-34 around middle of body; no supranasals; a transparent eye disc; legs short failing to meet by a distance greater than length of arm; lateral stripe broken into 20 to 22 spots between shoulder and groin; dorsum with numerous small rounded spots scattered on all scalerows; one or two pairs of feebly-enlarged nuchals; tail long, nearly one and three-fourths times snout-vent length.

Description of species (from No. 20611, Boonsong Lekagul, Coll.): Body slender; snout narrow; rostral broader than high forming a nearly straight suture with frontonasal; prefrontals forming a median suture, broadly in contact with both loreals; frontal longer than its distance from tip of snout, shorter than length of combined parietals; two frontoparietals, slightly larger than interparietal which is inclosed by large parietals; two median scales following

parietals somewhat enlarged and might be regarded as nuchals; parietals bordered also by a secondary and a tertiary temporal; nasal diagonal, partly or completely divided by nostril, anterior part largest; first loreal much higher than long, curving forward; second loreal somewhat quadrangular; two small preoculars and two presuboculars, second wedged between fourth and fifth supralabials; one primary temporal, two secondary and three tertiary temporals; seven supralabials; six infralabials; first pair of chinshields broadly

FIG. 91.—*Leiolopisma cunice* Cochran, EHT-HMS No. 31785 (4390) Ban Muang Khai, Thali, Thali, Loei province, Thailand. Actual snout-vent length, 43 mm., total length, 49 mm.

in contact, second pair separated by one, third pair by three scales; four supraoculars, seven supraciliaries.

Eye with a transparent disc; ear-opening large, about two-thirds times diameter of eye; tympanum not deeply sunk; no auricular lobules.

Scales in 32 rows around middle of body, dorsal rows only a little larger than laterals, and equal or slightly smaller than posterior ventrals; a pair of enlarged preanal scales flanked by a smaller pair; fourth toes with 15-17 obtusely keeled lamella below; 92 subcaudals; 78 scalerows between parietals and a point above vent; adpressed arm and leg separated by about 18 transverse scalerows.

Color in life: Above olive, with scattered small black spots on all scalerows suggesting dim lines since space between spots is slightly darker; outer scalerow on dorsum somewhat lighter but no distinct stripes present; a narrow black line on side of snout, continues behind eye to a considerable distance on tail but becomes broken up into more than twenty spots on side and even more on tail, the spots completely or partially separated by golden or vertical cream lines; chin and venter somewhat dirty greenish white, the greenish color more pronounced posteriorly under tail.

Measurements in mm.: Snout to vent, 41; tail, 72; length of head, 9; width of head, 5; snout to ear, 7; snout to arm-insertion, 13.2; axilla to groin, 24; arm, 7.2; leg, 12.

Distribution: Known from "Pak Jong (= Pakchong), Dong Paya Fai Mts."; Doi Angka", Mai Hong Son, and Loei.

Addenda: Three specimens were examined in the British Museum: No. 1916.3.26.27 and 1916.27.29. The first specimen is the largest and measured 48 mm. snout to vent. The prefrontals form a board suture and there are 32 scalerows, and two pairs of nuchals. No. 1916.3.27; in this there are three pairs of small nuchals, the prefrontals are separated and there are 30 scalerows around middle. The lateral stripe is broken into 27 spots on the body. The legs fail to touch by 5 mm. ±; the snout-vent length is 47 mm. These are both from Pakchong near the type locality. One specimen, No. 1916.27.29, from Krabin, Siam, has five pairs of small nuchals. The ear-opening is nearly the size of the eye-opening.

Leiolopisma smithi Cochran

Leiolopisma smithi Cochran, Copeia, 1941, No. 4, Nov. 21, 1941, pp. 238-239, fig. 1 (type-locality, Kuhn Tan, ?Lampang province, Thailand).

Diagnosis: Dorsal scales distinctly larger than laterals in six rows across back, the gradation into lateral scales not abrupt; three rather irregular pairs of nuchals; snout moderately short, obtusely rounded; no light vertebral stripe; 28 scalerows about middle of body; venter not white. Allied to *Leiolopisma doriae* but differing in ventral coloration, shorter frontal, and in wide contact between prefrontals.

Description of species (from type description): Distance between end of snout and arm-insertion contained one and one-half times in axilla to groin distance; no supranasals; frontonasal much broader than long, widely separated from frontal by prefrontals which are widely in contact; frontoparietal divided; an interparietal; frontal

three fifths as long as frontoparietals and interparietals together; parietals forming a short suture behind interparietal; three rather irregular pairs of nuchals; seven supraciliaries; four large supraoculars; seven supralabials, fifth and sixth below eye; ear-opening much larger than palpebral disc; no lobules; body scales smooth, the dorsals twice as long and twice as wide as laterals; 28 scalerows around body, six across back between lateral dark stripes; a pair of enlarged median preanals; tail reproduced; adpressed limbs barely fail to meet; digits long, 18 smooth lamellae or very bluntly keeled lamellae under fourth toe.

Color in alcohol: Dorsum metallic sepia; a dark clove-brown dorsolateral line beginning at nostril continuing behind eye, above ear and along sides to tail, interrupted behind axilla so that it appears as a series of irregular dark spots on posterior body and beginning of tail. Venter immaculate drab-gray; sides of head, lips, upper surface of arms and legs heavily spotted with clove-brown.

Measurements in mm.: Head and body, 48; width of head, 6; head length, 10; tip of snout to arm-insertion, 18; tail (part reproduced), 56; axilla to groin, 28; arm, 11; leg, 16.

Distribution: Known only from the type-locality.

Remarks: Dr. Cochran suggests that two specimens reported by Dr. Malcolm Smith from Doi Suthep, referred provisionally to *L. doriae* may belong here. If this is true *doriae* would be deleted from the Thai list of species.

Leiolopisma tavesae M. Smith

Leiolopisma tavesae M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 298 (*part.*) (type-locality, Bong Tee Valley west of Kanburi [= Kanchanaburi] Thailand); Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, p. 1042 (listed only).

Diagnosis: A small leiolopismid; two frontoparietals; 24 (28) scalerows around body; limbs short, failing to touch when adpressed by a distance nearly equal to the length of arm; snout to vent length, 38 mm. No nuchals; eight supraciliaries; preanals large; anterior loreal larger than posterior or subequal.

Description of species (from the type, British Museum No. 1933.12.1.1): Rostral broadly visible from above forming a broad suture with frontonasal; latter much broader than long, touching loreal laterally, forming a suture with frontal, and separating prefrontals; frontal narrowed posteriorly, its length much greater than its distance from tip of snout, shorter than its distance from posterior

end of parietal; no widened nuchals; nostril in a single nasal; a single large loreal (fusion of first and second), followed by two small superimposed preocular scales normally present in the genus; three small presuboculars; four supraoculars; eight supraciliaries; three or four small postsuboculars; one anterior, two large secondary, and three tertiary temporals; seven supralabials, fifth below median part of eye; lower eyelid with a transparent disc; ear very large, tympanum rather superficial, much larger than transparent disc, its diameter (1 mm.) much smaller than length of eye; mental border on lip greater than that of rostral, followed by a large postmental, in turn followed by paired chinshields in contact, a second pair separated by one scale, and a third pair separated by three scales.

Scalerows around body at middle, 24;* about 64 scales from parietal to a point above vent; two large preanals extending distinctly farther posteriorly than adjoining scales; subcaudals, 81, median row a little larger than adjoining rows but not distinctly widened transversely; arm and leg small, failing to overlap by nearly length of arm; third and fourth fingers of nearly equal length, each with eight lamellae; leg longer than arm, fourth toe considerably longer than third, and with 14 or 15 lamellae.

Color: Above light brown with indistinct darker lines of spots suggesting dim lines on back, the marks continued dimly onto tail; a somewhat wider more distinct line from nostril to eye, and from eye along dorsolateral region of body; sides of neck and lower parts of sides with lines of darker dots indicated. Whitish below.

Measurements in mm.: Snout to vent, 40.2; tail, 64; width of head, 5.2; length of head, 10; snout to arm insertion, 13; axilla to groin, 23; arm, 7; leg, 10.2.

Variation: Two other specimens were referred by M. Smith to this species, one of which is from somewhere in peninsular Thailand. It differs in having 28 scalerows around middle of body instead of 24; there are certainly 2 distinct loreals both a little lower than the single one of the type of *tavesae;* a pair of nuchals are present while there are none in *tavesae.* There are 69 scales from parietal to above vent. The ear-diameter is .7 mm., the eye length 1.4 mm.

The color appears to differ in that on each side of the back there is a dorsolateral lighter line extending from the eye along body and on to tail (but most of tail broken and lost); between these two lines there are six distinct brown dotted lines. The darker

* I count only 24 scalerows around middle of body; also I find only one instead of two loreals.

lateral stripe is two scales wide and (perhaps a third scalerow is slightly darker also), below which the ground color is light brown and the scalerows bear rows of dots indicated even on outer ventral row. The sides of the neck also have distinct rows of dots.

There is enough difference between these specimens as to cause one to question whether they should all be regarded as the same species.

A third specimen presumably of this form is mentioned, from Pegu, Burma. Of this specimen Dr. Smith says, "The loreals are as in the second specimen but in other respects it agrees with the type." This specimen I have not seen.

Distribution: Known only from the above mentioned localities.

Leiolopisma kohtaoensis Cochran

Leiolopisma kohtaoensis Cochran, Proc. Biol. Soc. Washington, vol. 40, 1927, pp. 188-190 (type-locality, Kao Tao, Island Gulf of Siam); Proc. U. S. Nat. Mus., vol. 77, 1930, pp. 20-21, fig. 5 (three drawings of head); M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 296-297.

Diagnosis: Limbs well developed, not meeting when adpressed in adults (may touch in young); ear-opening oval, little smaller than eye-opening, without lobules; a transparent palpebral disc; no supranasals; two frontoparietals one or more pairs of nuchals; 30 somewhat irregular scalerows around middle of body.

Description of species (from type description): Body elongate, distance from tip of snout to arm-insertion in axilla-to-groin distance one and three-fifths times; snout short obtuse; a transparent palpebral disc; nostril in a single nasal; no supranasals; frontonasals broader than long; prefrontals forming a median suture; frontal two-thirds of length of combined parietals; four supraoculars; seven supraciliaries; frontoparietal divided, the parietals forming a suture behind interparietal; ear-opening oval a little smaller than eye-opening; no auricular lobules; nuchal region with one or more pairs of irregularly enlarged scales; 30 scalerows about body, smooth, rather irregular, so that 31 or even 32 scales may be counted in places; lateral scales smallest; median subcaudals very slightly enlarged except where tail is reproduced; large pair of preanals; when adpressed, limbs separated in adults by a distance equal to length of fingers; 16 lamellae under fourth toe.

Color: Light bronze on dorsum with irregular scattered dark brown spots on top of head and in the centers of some dorsal scales; a dark brown band starting on canthus, passing above ear, widening

on shoulder, and broken regularly by small bars of lighter color invading it; on tail, band lighter and broken up into spots; on sides, below this dark band, pinkish yellow with a quite irregular row of small dark brown dots along the lateroventral line; arms and legs spotted and irregularly banded above. Undersurfaces white, immaculate except for few small brown dots on throat; lips spotted brown.

Measurements in mm.: Snout to vent, 44; tail reproduced, 41; axilla to groin, 24; snout-tip to arm-insertion, 15; arm, 9; leg, 13.

Variation: The length of the prefrontal suture varies a little, and in the young the adpressed limbs touch. The size of the interparietal varies. The nuchals vary, a single pair or three pairs may be present, the type has two. The number of lamellae under the fourth toe varies between 15 and 17.

Distribution: Known certainly only from the island of Koh Tao. Malcolm Smith has tentatively referred a specimen from Nakhon Si Thammarat, having 28 scalerows about the body to this species.

Remarks: The type of *kaotaoensis* (U.S.N.M. No. 72284) has been examined, as well as the paratypes. The dorsal scales of female specimens, distended with eggs seem to be considerably larger than those on males. This is of course due to the fact that in imbricate scales, stretching of the skin exposes more of each scale.

Leiolopisma siamensis Taylor and Elbel

Fig. 92

Leiolopisma siamensis Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1123-1125, fig. 20 (type-locality, Phu Kho Mountain, 522 M. Kan Luang, Na Kae, Nakon Phanom province, Thailand).

Diagnosis: Prefrontals meeting or forming a strong suture; no supranasals; undivided disc on lower eyelid less than one third of the size of ear; preanals enlarged; a pair of small nuchals flanked by a larger one laterally; no spotting on back; about 65 scales from parietal to above vent; two anterior temporals; two secondary temporals; some dark spots on shoulder laterally with a slight dorsolateral light line present or absent; 34 scalerows about middle of body.

Description of species (from 34934): Rostral large, broadly in contact with frontonasal; latter nearly twice as wide as long touching anterior loreal and nasal laterally; two prefrontals, broadly in contact, touching both loreals; frontal narrowed posteriorly, its length greater than its distance from tip of snout, shorter than combined

parietals; parietals broadly in contact behind interparietal; four large supraoculars, two touching frontal, first in contact with prefrontal; nostril in a single nasal; no postnasal; two loreals, anterior higher and slightly narrower than second; two "preocular" scales, lower much like a third loreal; two presuboculars, nine supraciliaries;

FIG. 92.—*Leiolopisma siamensis* Taylor and Elbel. No. 34934, Forestry station, Sanoi River, Ubon province, Thailand. Actual total length, 131 mm.; snout to vent, 50 mm.

seven supralabials, fifth and sixth under eye, sixth separated from large secondary temporal by two anterior temporals; seventh labial separated from it by one scale; tympanum large, rather deeply sunk, with three minute lobules visible; six infralabials; mental white with a slightly larger labial border than rostral; an azygos postmental; three pairs of chinshields all touching labials, first in contact, second separated by one scale, third by three scales, fourth pair small, scarcely differentiated.

The ear-opening somewhat more than three times as large as transparent disc in lower eyelid; nuchal very small and probably should not be regarded as a true nuchal.

Scalerows, 34 around middle of body, dorsal and lateral scales subequal; about 65 scales from parietal to a point above vent; distal three fourths of subcaudals wider than adjoining scales; 101 subcaudals, distal 37 regenerated and more widened than others. When limbs are adpressed toes reach wrist or a little beyond; 19-20 lamellae under first toe.

Color in life: Rather olive-brown with darker areas in supraocular region; faint trace of lateral dark line behind eye to shoulder; dorsolateral light line apparently not present; ventral surfaces whitish, subcaudal region with a wash of pink.

Measurements in mm. of *Leiolopisma siamensis*

NUMBER	Type	34934	35017	35016	34903
Snout to vent	51	50	51	48	50
Tail	65*	81*	66.5*	42**	45*
Snout to ear	.....	10	9.6	9.6	10
Head length	13	12.5	11.8	11.6	11.8
Head width	7.3	7.2	7.2	7.2	7
Snout to arm	19	19.2	18.3	18.6	18.2
Axilla to groin	24.5	27	23	23.5	26
Arm	14	13	13	12.8	12.5
Leg	20	19	19	18.2	17.2

* Tails regenerated; ** tail broken.

Distribution: Known from the type locality, Nakhon Phanon, Udon Thani, and Ubon (Nos. 34934, Sanoi River, Ubon; 34903, Ubon City; 35016, 35017, mountain west of Udon Thani, city).

Remarks: One specimen, No. 35016, shows three or four strong dark spots on shoulder in front of arm-insertion and one or two spots posterior to it; there are also very dim spots discernible extending from these to base of tail. Two of the specimens show a

single widened pair of nuchals which is probably the normal condition. All the specimens have the prefrontals broadly in contact.

In the type diagnosis the statement "fifth labial separated from it by one temporal scale" should read "seventh labial separated from it by one temporal scale." In measurements, "axilla to grain" should read "axilla to groin."

Leiolopisma melanostictum Boulenger

FIG. 93

Lygosoma melanostictum Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 5, 1887, pp. 479-480 (type-locality Pla-poo, Tenasserim, Burma, referred to the section *Leiolopisma*); *ibid.*, ser. 2, vol. 13, 1893, p. 230; The fauna of British India including Ceylon and Burma; Reptilia and Batrachia, 1890, p. 199 (hills of northern Tenasserim, between 3300 and 4000 ft.); ?Flower, Proc. Zool. Soc. London, 1899, p. 650 (38 smooth scales around middle of body [*part.*]); ? Schenkel, Verh. Ges. Basel, vol. 13, 1901, p. 190; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, June, 1916, p. 56 (*part.*); *ibid.*, Dec., p. 157 (Nakhon Si Thammarat; scales usually 38).

Leiolopisma reevesii melanostictum: M. Smith, The fauna of British India . . . Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 296-297 (*part.*)

Diagnosis: A medium sized specimen (50 mm.) with numerous black punctations on back on either side of midline; scales in 36-38 rows; most scales of side of head, neck, flanks, and lower sides of tail with dark flecks tending to form lines. When limbs are adpressed the toe reaches hand but not quite to wrist; frontoparietal divided; no enlarged nuchals; prefrontals broadly in contact; lateral dark stripe begins narrowly near tip of snout, continues onto tail, but partially broken throughout, lower edge very indefinite; 18-19 lamellae under fourth toe.

Description of species (from No. 35906, Doi Suthep, Chiang Mai): Rostral nearly twice as wide as high, forming an elongate, slightly curved suture with frontonasal; frontonasal once and a half times as wide as long, separated from frontal by large prefrontals broadly in contact, touching first loreal laterally; frontal narrowed posteriorly about as long as distance to tip of snout, much shorter than combined parietals; frontoparietals paired; interparietal as wide as long, broadly inclosed by parietals; no broadened nuchals; four supraoculars, two touching frontal, first touching prefrontal; seven supraciliaries; lower eyelid with a small, somewhat elongate transparent disc; two loreals, anterior the higher and equally as broad as the second; two presuboculars, third wedged between fourth and fifth supralabials; seven supralabials, sixth largest separated from enlarged upper temporal by a single scale, seventh separated from

FIG. 93—*Leiolopisma melanostictum* Boulenger. Both from Doi Suthep, Chiang Mai province. Left figure, 35906. Actual total length, 137.5 mm.; snout-vent length, 49.5 mm. Right figure, 33780. Actual snout-vent length, 49.5 mm.

it by one scale also; ear large, tympanum not deeply sunk lacking lobules; scales in 36 rows around body; scales of postoccipital region scarcely wider than on back; eight scalerows between lateral dark stripes; six infralabials, the fifth largest; an azygos postmental and four pairs of chinshields, first pair touching, second separated by one scale, all in contact with infralabials; adpressed arm and leg overlap the length of fingers; 19 lamellae under fourth toe; subcaudals on distal three fourths of tail wider than adjoining scales; 76 scales from parietals to a point above vent.

Color: Above dark brown with very numerous small black dots; a slightly lighter brown dorsolateral line extending onto shoulders confined to one scalerow which is separated from its fellow by six scalerows; dark flecks on most of dorsal head scales; a lateral line beginning narrowly on snout passing partly above eye and ear-opening and continuing on side of body and less distinctly along sides of tail the lower edge rather indefinite throughout, and bearing scattered distinct light spots or indefinite lighter areas. Scalerows of sides, neck, side of head, and tail bearing numerous dark flecks sometimes encroaching on ventral area; seven ventral scalerows whitish lacking spots; chin scales and underside of neck with a few flecks. Arms and legs reticulated, enclosing lighter spots and areas.

Table of data on *Leiolopisma melanostictum*

NUMBER (sex)	33780	35906 ♀	3680 ♂	3681
Snout to vent length	49.5	52.5	49	43
Tail length	.....	85	.....	.....
Snout to arm insertion	18	16.7	17.6	15
Axilla	27.8	30	28	23
Arm	12	12.7	14	11
Leg	19.8	19	19.6	17
Scales around middle	36	36	36	36
Scales parietal to above vent	74	76	74	75
Lamellae 4th toe	19	19	19	19–20
Prefrontals, broad contact	yes	yes	yes	yes
Nuchals	no	no	no	no

Variation: The table shows variation. The females appear to have a slightly longer axilla to groin measurement.

Distribution: The species occurs in the mountain ranges along the boundary of Burma and Thailand and usually at an elevation between three and four thousand feet. My specimens are from Doi Suthep, Chiangmai province. I have not seen the specimen re-

ported from Bangkok and "Chantaboon" but suggest that these be re-examined.

Remarks: I do not consider this form to be a subspecies of *reevesii*.

Leiolopisma rupicolum (M. Smith)

Fig. 94

Lygosoma rupicola Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, 1916, pp. 45-46, pl. fig. 3 (type-locality, Chong Kae, near Paknampo, central Thailand).

Leiolopisma rupicola: The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, Feb. 7, 1935, p. 297; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1119-1121, fig. 18 (Nakon Phanom).

Diagnosis: A disc on eye much smaller than large ear-opening; leg reaches beyond elbow of adpressed arm; no supranasals.

Description of species (from No. 33338 near Muk Lek, Nakhon Ratchasima prov.: Snout obtusely pointed. Rostral broadly visible above, forming a straight suture with frontonasal; prefrontals large, broadly in contact, touching both loreals equally; four supraoculars, two in contact with frontal; frontal as long as its distance from tip of snout, shorter than frontoparietals and interparietal together; narrowed to a point posteriorly; frontoparietals distinct, a little larger than interparietals; latter scale enclosed by parietals; no elongate nuchals following parietals but a series of larger scales border them between temporals; nostril in a single nasal scale; two large loreals, anterior the higher; two preoculars, lower largest, and two presuboculars, the latter one wedged between the fourth and fifth supralabials; seven supralabials, fifth, below eye, largest; six or seven infralabials; ear-opening much larger than eye-disc; dorsal scales about size of those on venter, but a little larger than lateral scales; no lobules projecting from edge of ear. Thirty-six scalerows around middle of body; legs and arms strongly developed, adpressed leg reaching beyond elbow of adpressed arm; 17 obtusely keeled lamellae under fourth toe; four enlarged preanal scales, two median distinctly the larger; 119 subcaudal scales; 71 scales from parietals to above vent.

Color in life: Above brown-olive to light brown covering median eight scalerows, outer rows a little lighter; laterally an indefinite dark line, varying in width, extends from eye backwards on side and reaches somewhat onto tail; top of head darker with some indefinite dark spots; two rows of dark spots on two median dorsal scalerows.

The lateral band is continuous anteriorly but on shoulder and sides it breaks up into spots separated by areas of lighter color; tail pinkish-olive growing more pink posteriorly; chin whitish; venter pinkish lavender, underside of tail yellowish, becoming pinkish towards tip; labials with faint dark marks along sutures; arms and legs mottled with dark brown or blackish, and light olive; below, limbs flesh with a slight yellowish wash.

In alcohol venter is largely violet, the subcaudal region pure white.

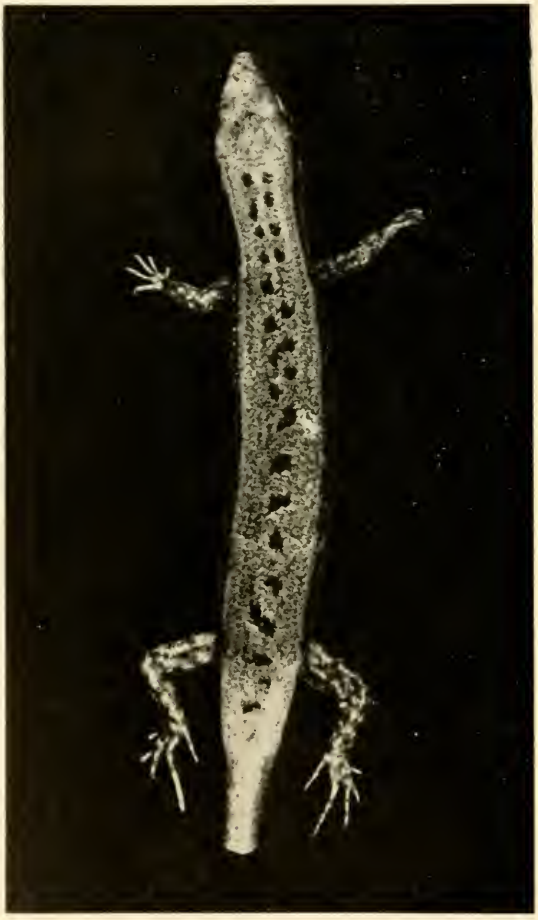


FIG. 94.—*Leiolopisma rupicolum* M. Smith. No. 786, Khao Phra Vihan, Ubon province, Thailand. Actual total length, 65 mm. to end of broken tail.

Measurements in mm.: Snout to vent, 38.5; tail, 65.5; width of head, 6; length of head, 9; snout to ear, 8; snout to arm-insertion, 15.4; axilla to groin, 19; arm, 11; leg, 17.

Variation: While the lateral coloration remains rather constant, the distribution of the spotting on the back varies considerably; the largest number of specimens have a double row of spots on the back anteriorly, the spots tending to fuse to make a single row posteriorly; one specimen from Sanoi River, Ubon, has a double row of spots anteriorly but from the middle of the back they are united to form a single median line that extends to near the tip of the tail. The supraocular areas are blackish. The other specimens show no lines or spotting on dorsal side of tail. The lamellae under the fourth toe varies between 17 and 19; the scales around the body vary between 34 and 36.

The largest specimen taken is from Khao Phra Vihan. It measures 53 mm. snout-to-vent. The part of the tail remaining has been regenerated. It is remarkable in having a series of broad, rather narrow scales in the subcaudal region, and a similar series on the dorsal part of the tail equal in size to the subcaudals—all symmetrical. Another feature of this specimen is a small symmetrical scale behind the frontal in contact with the second and third supraoculars. Since the frontal normally touches only the first two supraoculars one presumes that the scale is, at least, partially segmented from the frontoparietals.

Distribution: The species is known from the type locality Ubon, Nakhon Phanom (522 m. on Phu Kho), Udon Thani, Sara Buri and Sisaket. Dr. Smith reports it also from "Hin Lap, Dong Paya Fai Mts. at 200 ft.; east Siam; and Huey Sapan, northeastern Siam." The specimen here described is from Pasadet, Sara Buri. Outside of Thailand it is known from the Langbian plateau in Annam.

Remarks: I have examined certain specimens from the Langbian Plateau. The specimens were marked much like *Sphenomorphus stellatus* that may occur in the same area. One specimen shows a light median streak, the dorsal spotting much reduced and a tiny pair of nuchals is present (B. M. 1935.11.5.B).

A specimen from northeastern Siam (Huey Sapon) (B. M. 1933.12.1.10.11) has the prefrontals separated and 16 lamellae under the fourth toe.

Leiolopisma doriae (Boulenger)

Lygosoma doriae Boulenger, Ann. Mus. Civ. Genova, ser. 2, vol. 4, 1887, p. 620 (type-locality, hills west of Bhamo, Burma); The fauna of British India . . . Reptilia and Batrachia, 1890, p. 201; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 502.

Leiolopisma doriae: Smith, The fauna of British India including Ceylon and Burma, Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 302-303.

Diagnosis: Three or four pairs of nuchals; seven or eight supraciliaries, 28-32 smooth scales round middle of body; a pair of large preanals; adpressed limbs do not quite meet or may reach wrist; two frontoparietals, tail one and three-fourths times length, snout to vent; with transversely enlarged subcaudals.

Description of species: Distance between the end of snout and arm-insertion one and one-third to one and two-thirds times in distance between axilla and groin; prefrontals narrowly separated or barely touching; frontal about as long as its distance from first nuchals; three or four pairs of nuchals; seven or eight supraciliaries; auricular opening much larger than the palpebral disc, without projecting lobules or granules. Body scales smooth, the dorsals not twice as large as laterals; 26-28 scales about middle (28-32 *fide* M. Smith), six across back; a pair of large preanals; tail one and three-fourths times as long as head and body; with transversely enlarged subcaudals; the adpressed limbs do not meet or may reach as far as wrist; digits long, 16-18, keeled lamellae beneath fourth toe.

Color: Bronze-brown or golden brown above with numerous small black spots; a dark brown stripe along the upper half of the flank and neck, much broken up by lighter spots; lower parts of flanks with small black spots; whitish below.

Measurements in mm.: Snout to vent, 58; tail "one and three-fourth times as long as head and body," 101. (After Boulenger, F. B. I. 1890).

Remarks: This species is included in the Thai fauna on the basis of two very young specimens from Doi Suthep, provisionally referred to this species by Malcolm Smith. This form has been reported from "Annam" by Bourret. This may be a questionable record, and I consider it doubtful that it occurs in Chiang Mai.

While visiting the Senckenbergian Museum in Frankfurt I examined the type (No. 14685) and recorded the following data: a narrow frontonasal wider than long touches frontal separating the prefrontals; frontal as long as its distance from snout, shorter than parietals and frontoparietals combined; frontoparietal divided; a small interparietal enclosed by parietals; three and one-half pairs

of nuchals; nostril a little behind suture of rostral and frontonasal; four supraoculars; six supraciliaries; one anterior temporal; two secondary temporals, the upper very large; two tertiary temporals, the two large; upper secondaries narrowly separated from each other; two loreals both same height; two presuboculars; seven supralabials the fifth below the eye; transparent disc in eyelid as large or larger than ear-opening; two large preanals; subcaudals, after six paired basal scales, distinctly widened; 16-17 lamellae under fourth toe.

Very nearly uniform brown-olive on dorsum with some brown flecks on dorsum and sides of tail; leg and foot with brownish marks; a brown line from nostril through eye and along side; dark brown area on upper arm and small bars on hand and fingers.

Genus Lygosoma Hardwicke and Gray

Lygosoma Hardwicke and Gray, Zool. Journ., vol. 3, 1827, p. 228 (type of genus *Lacerta serpens* = *quadrupes*.

Diagnosis: Palatine bones in contact mesially; ear-opening reduced; limbs pentadactyl but greatly reduced in size and widely separated.

Only a single species, *Lygosoma quadrupes* (Linnaeus) of this genus is recognized in Thailand.

Lygosoma quadrupes (Linnaeus)

Fig. 95

Lacerta chalcides Linnaeus, Systema Naturae, 12th ed., 1766, p. 369.

Anguis quadrupes Linnaeus, Systema Naturae, 12th ed., 1766, p. 390 (type-locality, Java).

Lygosoma quadrupes: Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 16; M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 290-291.

Scincus brachypus Schneider, Historiae amphibiorum naturalis et literariae, fasc. 2, 1799, p. 192.

Seps pentadactylus Daudin, Histoire naturelle générale et particulière des reptiles, vol. 4, 1802, p. 325.

Lygosoma abdominalis Gray, Ann. Mag. Nat. Hist., vol. 2, 1839, p. 332 (type-locality, India, Java).

Lygosoma brachypoda Dumèril and Bibron, Erpétologie générale . . ., vol. 5, 1839, p. 721 (type-locality, Java).

Lygosoma chalcides: Gray, Catalogue of the specimens of lizards . . ., 1845, p. 88; Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 340; A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, p. 97; M. Smith, Journ. Nat. Hist. Siam, vol. 2, Dec. 1916, p. 157 (Nakhon Si Thammarat, "Bangnara, Patani"); *ibid.*, June, 1961, p. 56 ("widely distributed, not uncommon in Bangkok").

Lygosoma (sec. Lygosoma) quadrupes: M. Smith, Rec. Ind. Mus., vol. 39, 1937, p. 221.

Diagnosis: A slender, diminutive skink, with four very short limbs and an elongate body; prefrontals separated; frontoparietal single; ear-opening minute, partly covered with scales; 24 to 26 scalerows around middle of body; five lamellae under fourth toe. The color is gray-brown to brown, with dark longitudinal lines, usually visible on edges of all scalerows, continued onto tail.

Description of species (from No. 33423, Bangkok): Body slender, head bluntly pointed; rostral little wider than high, frontonasal broader than long, forming suture with rostral, frontal, and anterior loreal; prefrontals small, widely separated; frontal little longer than wide, little longer than its distance from tip of snout, about as long as single frontoparietal, but smaller; interparietal a little smaller than frontal, pointed posteriorly, enclosed by parietals; nuchal present on right side (broken in two on left); nasal single; no postnasal; anterior loreal higher but narrower than second loreal; small preocular with a continuous series of pre-, sub-, and postoculars the anteriormost largest; four supraoculars, three touching frontal; two anterior temporals, upper touching parietal; six supraciliaries; seven supralabials, anterior longest; six infralabials; mental with a longer labial border than rostral; an undivided postmental; first chinshields in contact; second pair separated by one scale; third pair only slightly enlarged, separated by three scales, and separated from labials by a small scale.

Twenty-six scalerows around middle of body, scales subequal; 115 transverse rows between parietals and a point above vent; subcaudals 106 (the extreme tip 4½ mm. regenerated); six preanal scales, two median largest.

Ear-opening narrow, partly covered with scales; lower eyelid movable, covered by two rows of scales. Arm short; four lamellae under three longest fingers, six under longest toe, three median toes nearly same length. Length of arm in axilla-to-groin measurement, eleven times.

Color in life: Above violet-brown to violet with darker lines bordering edges of all scalerows, somewhat less distinct above, more distinct on sides and venter where ground color is whitish or white, the dark lines continuing to tip of tail. Upper labials rather dark, the color not uniform and sutures may be lighter. Top of head darker than body; lower eyelid nearly yellow-white.

Variation: A specimen taken at a point 2 km. west of Kanchanaburi, Kanchanaburi province in a limestone hill showed certain differences which may be of some significance. The specimen is a

large female measuring 68 mm. snout to vent. with a scale count (parietal to above vent) of 121, six more than appear in other specimens examined. The arm measures 3 mm.; the axilla-to-groin measurement is 54.

The specimen, however, has very short arms and legs when compared with specimens from Bangkok. and Ang Hin, Chon Buri province, although in many, if not all skinks the limbs when present attain their growth earlier and seemingly fail to grow at their

FIG. 95.—*Lygosoma quadrupes* (Linnaeus). No. 4029, Ang Hin, Chon Buri, Thailand. (Young.) Actual length, 95 mm.

Measurements in mm. and scalecounts of *Lygosoma quadrupes*

NUMBER	33423	33282	33473	33540	33113
Snout to vent	59	50	68	61	43
Tail	68*	54*	64*	69*	37*
Width of head	4.1	3.7	4.6	4.2	3.7
Width of body	4.1	3.7	5.2	4	3.7
Snout to ear	5.7	5.6	6.3	6.1	5.4
Snout to arm insertion	12	11.2	12.2	12	9.3
Axilla to groin	44	37	54	42	29.4
Arm	4	3.25	3	3.6	3.1
Leg	4.9	4.6	4.3	5	4.8
Scales parietal to vent	115	115	121	115	114
Subcaudals	106*	109*	96*	118	89*
Scales around body	26	28	26	24	26

Nos. 33423, 33540, Bangkok; 33282, 33113, Ang Hin, Chon Buri; 33473, Kanchanaburi.
* Incomplete tails.

regular rate after adult size is reached. However, in this specimen the arm is as short as that of a specimen with a snout-vent length of only 43 mm. The fingers are relatively shorter also. The coloration of the venter is nearly pure flesh with the longitudinal lines only showing dimly at sides of venter; the subcaudal region also is rather light in color.

Scalerows vary from 24 to 26 around the body in the series examined.

Distribution: This species has been found in Thailand in the following provinces: Sara Buri, Ayutthaya, Phra Nakhon, Kanchanaburi, Pattani, Yala, Chon Buri, Nakhon Si Thammarat, Prachuap Khiri Khan, Songkhla, and Trang. Why it should seemingly be absent in the central and eastern parts of Thailand is difficult to explain since it occurs outside of Thailand in South China, Indo-China, Malay, the Indo-Australian Archipelago as far east as Palawan in the Philippine Islands.

Genus SAIPHOS Gray

Saiphos Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9, 1831, Synopsis, p. 72 (type of genus *aequalis*).

Diagnosis: An undivided transparent disc on lower eyelid; no supranasals; no auricular opening but a depression in position of ear; limbs pentadactyl short, not overlapping when adpressed.

The species has been found only once in Thailand.

Saiphos quadrivittatum (Peters)

Lygosoma (Cophoscincus) quadrivittatum Peters, Monatsb. K. Akad. Wiss. Berlin, 1867, p. 19; *ibid.*, 1872, p. 583 (type-locality, Mindanao, P. I.); Boulenger, Catalogue of the lizards in the British Museum, vol. 3, 1887, p. 329; Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 159 ("Bukit Besar, Patani States"); The fauna of the Malay Peninsula, from the Isthmus of Kra to Singapore; Reptilia and Batrachia, 1912, pp. 95-96; M. Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, June, 1916, p. 56 (Bukit Besar, "Patani States" = Pattani); Bull. Raffles Mus., no. 3, 1930, p. 38.

Siaphos quadrivittatum: de Rooij, The Reptilia of the Indo-Australian Archipelago . . ., vol. 1, 1915, p. 271; Taylor, The lizards of the Philippine Ids., 1922, p. 223.

Diagnosis: Diminutive skinks, snout to vent, 37 mm.; limbs pentadactyl, not meeting when adpressed; lower eyelid with an undivided transparent disc; no supranasals; single frontoparietals; small frontal; three to four pairs of nuchals; ear hidden; 18 to 20 scales about body.

Description of species: Distance between end of snout and arm-insertion one and one-half times in distance between axilla and groin; limbs well developed, pentadactyl, not meeting when adpressed; snout rather pointed, frontonasal touching rostral; no supranasals; prefrontals small, separated; frontal scarcely longer than single frontoparietal; parietals forming a suture behind interparietal; three or four pairs of nuchals. Fifth supralabial below eye; auricular opening hidden under scales, indicated by a depression; nostril in a single nasal; 18 to 20 smooth scales around body at middle, two dorsal rows largest; two preanals slightly enlarged; digits slender, fourth toe longest, with 15-16 lamellae on undersurface; lower eyelid with an undivided disc. Tail thickened a little shorter than head and body; limbs rather short, overlapping when adpressed.

Color in life: Yellowish or yellowish orange to pale brown above, with four blackish longitudinal stripes, median pair extending to supraoculars; lateral pair extends to eyes; digits with dark crossbars; undersurface yellowish or brownish white; lips, chin, sides of head, and neck spotted with black; tail dark spotted, the spots sometimes making vertical bars on side.

Measurements in mm.: Snout to vent, 37; tail, 35.

Distribution: The species is included in the fauna of Thailand on the basis of a collection made in the extreme southern part of Thailand at "Bukit Besar, Patani States."

It is a widespread species, being known in Malaya, Borneo, Australia, Celebes, and the Philippine Islands.

Ophioscincus Peters

Ophioscincus Peters, Mon. Akad. Berlin, 1873, p. 747 (type *australis*).
Typhlosaps Angel, Bull. Mus. Hist. Nat. Paris, 1920, p. 4 (type *roulei*).

Diagnosis: Palatine bones in contact mesially; pterygoid bones in contact anteriorly, palatal notch far back in mouth; maxillary teeth conical; no pterygoid teeth. Eye small, lower eyelid composed of one or two thickened scales, probably immovable; no upper lid. Nostrils situated in anterior part of a very large nasal; no supranasals; frontonasal present; frontoparietals distinct; no ear-opening. Body vermiform; no limbs; vestiges of pectoral and pelvic girdles.

Two species of this genus are known in Thailand. These are *Ophioscincus anguinoides* and *Ophioscincus roulei*. They may be distinguished by the following key:

KEY TO THAI SPECIES OF OPHIOSCINCUS

Nasal shields separated or barely touching one another; 22 to 24 scales around body ..... *anguinoides*
Nasal shields broadly in contact; 18 scalerows around body ..... *roulei*

I have been unable to accept the placing of Lönnberg's *Isopachus* as a synonym of this genus as proposed by Malcolm Smith. While I am certain that *roulei* and *anguinoides* are congeneric I am not wholly certain that they in turn are congeneric with the Australian *australis*. This placement acknowledges an enormous gap in the continuity of distribution of this genus.

Ophioscincus anguinoides Boulenger

FIG. 96

Lygosoma anguinoides Boulenger, Journ. Nat. Hist. Soc. Siam, vol. 1, 1914, p. 67 (type-locality, Bangtaphan, "Patiyu State" Siam = Prachuap Khiri Khan province); Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 1, 1916, p. 56; *idem*, Dec. 1916, pp. 157-158; Cochran, Proc. U. S. Nat. Mus., vol. 77, 1930, p. 16 (Koh Tao [island] Gulf of Siam).

Ophioscincus anguinoides: Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 334-335 (Hat Sanuk, Klong Bang Lai, Bangtaphan, Maprit, localities between 10° 30′ and 12° N. Lat.).

Rhodona anguinoides M. Smith, Rec. Ind. Mus., vol. 39, p. 231.

Diagnosis: No limbs; body slender; tail about as long as head and body, ending in a point; no supranasals; frontonasal present, large; nasals touching or barely separated; frontal about size of frontonasal; prefrontals present, widely separated; frontoparietals broadly in contact, each as large as interparietal; 22-24 scales about

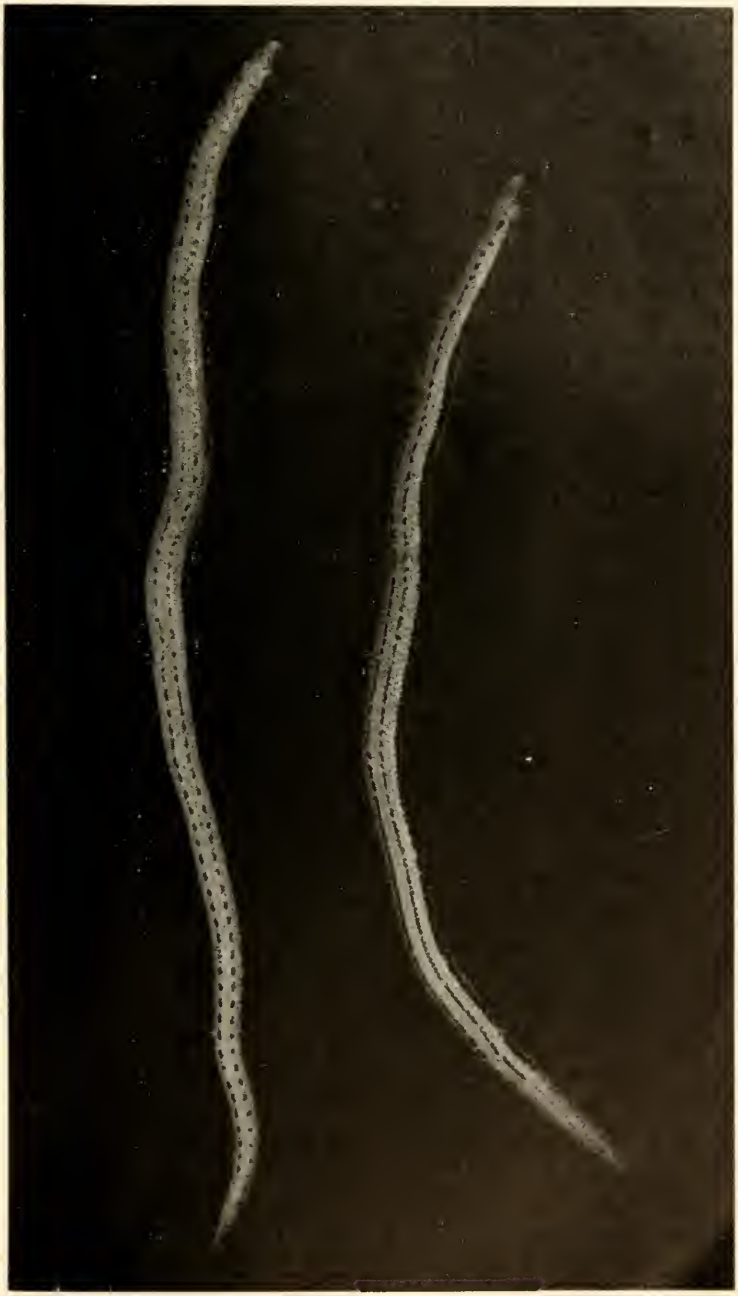


FIG. 96.—*Ophioscincus anguinoides* (Boulenger). Left figure, No. 606, Hua Hin, Prachuap Khiri Khan, province. Actual total length, 124.5 mm. Right figure No. 604, same locality. Actual total length, 113 mm.

middle of body; preanals enlarged; gray or gray-fawn above with two black dotted lines extending to tail; a dorsolateral dark stripe; venter and subcaudal region with dark lines on edges of scalerows.

Description of species (from No. 606, Hua Hin, Prachuap, Khiri Khan, Thailand): Body slender, head not strongly differentiated from body; rostral large, its apex prolonged backwards onto top of head, forming an angle; nostril pierced near anterior outer edge of nasal, slightly anterior to posteriormost lateral extension of rostral; nasals forming a median suture scarcely more than half length of scale; frontonasal broader than long, slightly angular on anterior border, touching loreal and prefrontal, forming a broad suture with frontal; latter larger than frontonasal, a little wider than long, touching two supraoculars. Frontoparietals large, broadly in contact behind frontal, scales nearly as large as interparietal; parietals slender, diagonally placed forming suture behind interparietal; well-defined pair of nuchals; first labial largest, touching loreal; extending farther back than nasals, followed by four labials, third below eye touching lower eyelid; one presubocular; two postsuboculars; four supraoculars, second widest pushing between frontoparietal and frontal; five supraciliaries; two primary temporals, one primary and one secondary temporal bordering parietals; mental large, its labial border only slightly larger than that of rostral; a large undivided postmental; five infralabials, first not or only slightly larger than fourth; two pairs of chinshields about same size, each separated by a single scale, and each scale in contact with infralabials; third pair of chinshields scarcely differentiated, touching infralabials, separated by five scales; a single ocular scale covers eye, bordered below by three or four granules; 27 scales around neck close behind head; 26 scales around middle of body; 15 scales around tail; two enlarged preanals; 94 subcaudals not or but slightly differentiated; no ear-opening; eye nearly or entirely concealed; head only slightly wider than neck. Rostral, nasals, first supralabials, first infralabials, and mental thickened; snout extending somewhat anterior to lower jaw.

Color: Gray-brown above, with a lateral stripe one and two half rows wide beginning on neck and extending to tip of tail; a pair of dorsal dotted lavender-brown lines, bordering edges of two scalerows, form lines from neck to tip of tail separated by two scalerows; edges of all scalerows on venter and subcaudal areas between lateral lines, more or less dotted with lavender, forming more or less distinct dotted lines, more distinct under tail; head with

numerous flecks above; an irregular black area about and in front of eye and on tip of snout under thickened terminal scales of snout.

Measurements in mm. of *Ophioscincus anguinoides*

NUMBER	603	604	605	606
Snout to vent	62	64	71	62.5
Tail length	44*	49*	?	62*
Total length	106	113		124.5
Width of head	4	4.4	4.4	4.1
Length of head	6.2	7	7	6
Width of body	4.5	4.9	4.5	4.6
Width of tail	4.1	4.3		3.9

* Regenerated.

Variation: My specimens differ but little in color and markings. The scalerows about body of all are 24 (25). Malcolm Smith (1935) reports 22-24. The nasals may be separated; there may be four or five supraciliaries, and four or five supraoculars; the scales about the body are subequal, the largest being on the tail. The dark color may be brown or lavender.

Distribution: The species is known only from a very limited region in peninsular Thailand, between 10° 50′ and 12° N. Latitude, chiefly in the provinces of Chumphon and Prachuap Khiri Khan. My specimens were taken at Hua Hin in the latter province near the sea shore on a golf course.

Remarks: These specimens were usually found under piles of rotting grass, or under other debris of various types; some, by digging in soft earth. Some were taken with *Isopachys gyldenstolpei.* (See under that species.) These lizards burrow with rapidity into soft earth. The species is endemic in Thailand and not known elsewhere. They are ovoviviporous.

Ophioscincus roulei (Angel)

FIG. 97

Typhloseps roulei Angel, Bull. Mus. Hist. Nat. Paris, 1920, p. 4, figs. (type-locality, "Siam").

Ophioscincus roulei: M. Smith, The fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, p. 335; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, 1958, p. 1043.

Diagnosis: Snout flattened anteriorly, somewhat wedge-shaped, the part visible above as long as internasal suture; nasals very large, broadly in contact mesially, the nostril in anterior lower part; a

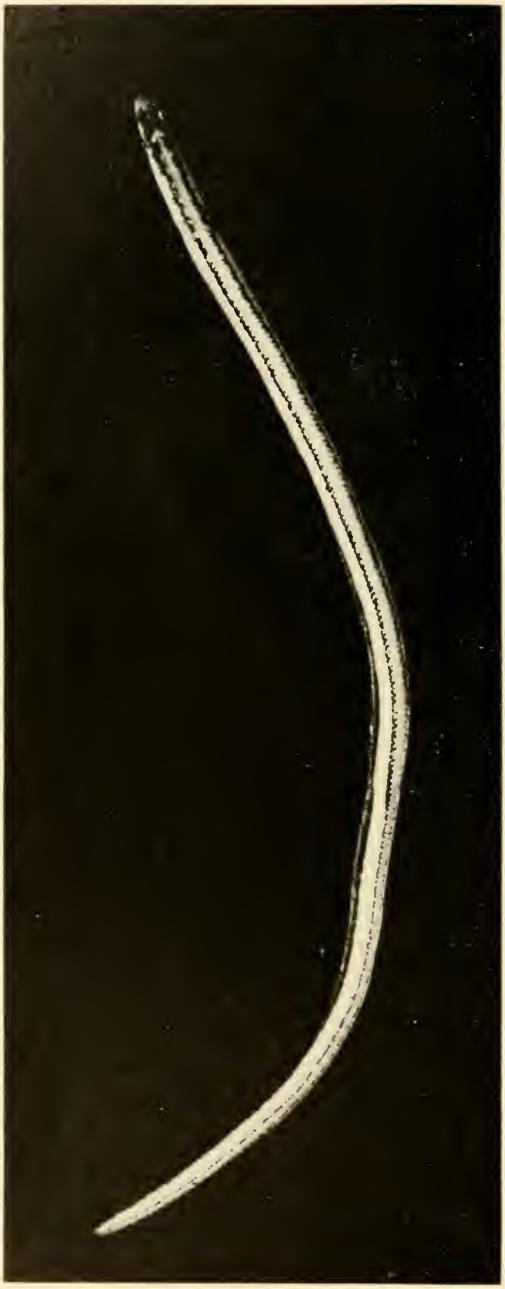


FIG. 97.—*Ophisaurus roulei* (Angel). From Bang Saen, Chon Buri, province. Approximately actual size.

frontonasal; prefrontals present; frontoparietals separated; a vertical depression on each side just back of head; limbs absent; 18 scalerows; head dark; body fawn to buff with two dark lines from occiput to end of tail; tip of tail blunt. Venter dark, the color extending well up on sides.

Description of species (from No. 33104, Ang Hin, Chon Buri province, Thailand): Snout narrowed, bluntly rounded, somewhat flattened above; rostral thickened, wedge-shaped, part visible above longer than internasal suture, very slightly shorter than nasals; latter large, broadly in contact, a little longer than broad, distinctly thickened, nostril situated in lower anterior part of scale; frontonasal twice as wide as long, touching one loreal laterally; prefrontals very small, widely separated from each other; frontal wider than long, slightly concave on anterior border touching prefrontal and one supraocular laterally, and forming a broad suture with frontonasal; frontoparietals separated, quadrangular, touching two supraoculars; interparietal larger than frontoparietals, broadly in contact with frontal; parietals rather narrow, elongate, enclosing interparietal; a pair of nuchals, wider than long.

Five supralabials, first largest, thickened, equally as long as nasals but extending a little farther posteriorly; second labial as high as first, touching loreal; a small preocular; third labial below eye; one postsubocular; two supraciliaries, three supraoculars; two anterior temporals, upper touching parietal, three secondaries, upper touching parietal and nuchal.

On sides of neck a vertical depression marking back part of head. Mental large, thickened, somewhat wider than long, with a longer labial contact than that of rostral; rostral projecting beyond mouth about a third the length of mental; four infralabials, first thickened; first chinshields separated by one scale, second by three scales, third pair by five scales.

Body scales in 18 rows about middle of body, 22 and 20 about anterior part; a pair of enlarged preanals flanked by a smaller scale on each side; scales from parietal to above vent, 125; subcaudals, 124, the last one an enlarged rounded scale.

Color in life: Slightly pinkish fawn above; lower part of rostral cream, clouded with darker above except at rim; nasals clouded; head dark with a T-shaped lighter area on frontal and frontonasal; two broad dark stripes begin on parietals and continue along back, narrowing, separated by two whole and two half scalerows; on tail edges of lines are diffuse and minutely broken; the median scale-

rows have minute blackish punctations and a few scattered punctations appear on the dorsolateral fawn rows; a short whitish line on temporal region; a blackish stripe borders the fawn from second labial, less intense anteriorly. This merges into dark brownish coloration of venter where all scales have some lighter areas; lateral dark line connected with narrow dorsolateral dark line just back of head. The preanal scales are partly grayish white.

Measurements in mm. (from Nos. 33104 and 33243, respectively): Snout to vent, 82, 92; tail, 71, 64; head, width, 3.2, 3.6; head, length, 6.1, 6.7; width of body, 3.85, 4; width of tail at base, 3.4; 3.3.

Distribution: The species originally was known from the two type specimens sent from Siam in 1883. The exact locality however was not known. This series represents the first definite localities. Bang Saen is a few kilometers south of Ang Hin in the same province, both localities being on the seacoast of the Gulf of Siam.

Remarks: A second specimen taken at the same exact spot as the described specimen at a later date, has the body and head somewhat lighter; the rostral, nasals, and first labials show but slight clouding and there is less dark pigment on the head. The dark lines on the back are less strongly marked, growing still fainter on the tail and the stripes on the sides are almost white. There is a faint powdering of brown on the venter and subcaudal regions. The tail is bluntly rounded and at the extreme tip it is almost as wide as the head. This is normal. The color above is light to the tip, while below the dark color of the ventrolateral lines unite to make the underside of the tip blackish. This is preceded by an indefinite white spot. This specimen was about four inches underground and was inadvertently severed while digging after another lizard (*Riopa*).

Specimens collected at Bang Saen, Chon Buri Apr. 15 and 18, 1958, were kept alive. On Apr. 21 one recently born young specimen was discovered in the vivarium. The other females containing embryos were examined. The young ones differed in degree of development.

Specimens taken at Bang Saen were in sandy soil in a coconut grove. When uncovered by digging about in a rotting coconut trunk or stump the specimens disappeared in the sand with alacrity seemingly by "swimming" in the sandy soil. They were not uncommon.

Genus ISOPACHYS Lönnberg

Isopachys Lönnberg, Kungl. Sven. Vet. Akad. Handl., Stockholm, Bd. 55, 1916, no. 4, p. 10, text figs. 2-6 (type *Isopachys gyldenstolpei*).

Palatine bones in contact mesially; maxillary teeth conical; no pterygoid teeth; eye small, closed, greatly reduced, the lower lid only slightly movable; nostril in anterior part of nasal; no supranasals, prefrontals or frontonasal; frontoparietal divided, the scales separated by an interparietal; limbless with at least a vestige of pelvic girdle present.

Only one species is known. It is endemic in Thailand, and presumably it is confined to a relatively small territory in the upper part of peninsular Thailand.

Isopachys gyldenstolpei Lönnberg

FIG. 98

Isopachys gyldenstolpei Lönnberg, Kungl. Sven. Vet.-Akad. Handl., Bd. 55, 1916, no. 4, p. 10, text figs. 2-6 (type-locality, Koh Lak, Prachuap Khiri Khan).

Ophioscincus gyldenstolpei: M. Smith, The fauna of British India, including Ceylon and Burma: Reptilia and Amphibia, vol. 2, Sauria; 1935, pp. 335-336, fig. 75.

Diagnosis: Snout broadened somewhat, much depressed, with a slightly angular edge, projecting forward beyond lower jaw; rostral large; nasals in contact; frontal very large, seven-sided; no supranasals; no prefrontals; no frontonasal; frontoparietals separated; the frontal and interparietal forming a suture; parietals relatively narrow, elongate, diagonal, forming a suture behind interparietal; rostral, mental, first supralabials, first infralabials and nasals much thickened, differing in color from rest of head.

Description of species (from No. 600 Hua Hin, Prachuap Khiri Khan, Thailand): Rostral rather large forming a flattened cap on snout extending forward beyond lower jaw, the posterior part forming an angle dorsally, laterally extending farther back than nostril; nasals very large, their sides curving rather than angular, forming a median suture equal to two thirds of their length; frontal as broad as long, its length much greater than its distance from nuchal or from tip of snout, in contact with interparietal; two frontoparietals, rectangular, widely separated by interparietal; parietals elongated, diagonally placed, forming a suture behind the interparietal; a pair of nuchals, left broken into two scales; a large

FIG. 98.—*Isopachys gyldenstolpei* Lönnberg. No. 600, Hua Hin, Prachuap Khiri Khan, Thailand. Actual total length, 250; snout to vent, 179 mm.

elongate secondary temporal borders parietal, upper primary temporal touches it also, but not lower; first supralabial very large extending farther back than nasals, followed by three supralabials, second, below eye, smallest; three supraoculars, median largest (not as shown in Smith's [1935] figure); two preoculars, one behind other (loreals?); one or two supraciliaries; a single opaque scale serves as a lower eyelid and presumably is slightly movable (seen in life); the interpretation of three other small scales below and behind the eye is in doubt. Mental very large with a labial border more than a half greater than that of rostral; an enlarged triangular first infralabial followed by three others; no azygos postmental; first pair of chinshields touch first infralabials, separated from one another by a small median scale; second pair not well differentiated, separated by several scales that are larger than adjoining scales, and also separated from infralabials. No ear-opening. A constriction behind head clearly defined laterally.

Scales smooth, 29 to 31 around neck; 24 rows at midbody, and 19 rows around the middle of the complete tail. Two median preanals distinctly enlarged but thin; lateral preanals somewhat modified; subcaudal count 85; proximally median row larger than adjoining scales, but more distally adjoining rows are equally widened.

Tail relatively short about one fourth of total length, terminating bluntly; tail at tip only slightly narrower than greatest body-width.

Color in life: Above, ground color pale yellow; dark lavender dots forming two dotted rows on the two median scalerows; a broad dorsolateral chocolate-brown stripe covering two whole and adjoining half rows of scales, these stripes tending to join on occiput; on tail, each stripe replaced by a series of indefinitely edged, quadrangular dark spots, separated by a narrow yellow line, the two rows separated by a yellowish line; side yellow; upper scalerows may have some minute dark dots; ten ventral scalerows light lavender brown, the edges slightly ragged, the stripe narrower on underside of neck. Top row of head yellow-brown with some darker marking about eye and a vertical mark on side of head.

Variation: The variation in scale counts around the middle of the body is 24 to 28 (*fide* M. Smith 1935). All specimens available to me have 24. Scales around the neck vary from 29 to 31, while around the middle of the tail the number is 19. Only one specimen has a complete tail and in this the subcaudal count is 85.

Variation noted in dorsal coloration is as follows: in Nos. 599 ♀ and 602 ♀ the two median rows of dots are moved outwards a

Measurements in mm. of *Isopachys gyldenstolpei*

NUMBER	599	601	600	602
Snout to vent	182	181	179	167
Tail	28*	61*	71	26
Total length	210	242	250	193
Diameter of body	9	10	9.9	9.8
Diameter of tail	7	9	8	8.8
Width of head	8	8.3	9	7.8
Length of head	12	11.3	12.3	9.9

* Regenerated.

little leaving an immaculate median line, the dots themselves tending to be attached to the dorsolateral stripe. In No. 601 the dots are minute, scattered, and do not form distinguishable lines.

In the No. 599 the dorsolateral lines fail to coalesce on the occiput; surrounding a light spot in this area there is a fine tracery of lavender. There are scattered lavender flecks on the head. The dorsolateral lines continue on the tail as a series of spots that tend to coalesce and form transverse bars divided medially; part of the tail is regenerated. In No. 601 there are 22 transverse bars, while the regenerated part of the tail shows three or four more indefinite bars. The sides of the tail may have a fine powdering of lavender.

Distribution: The species has been known previously from three specimens taken at Kho Lak, the type-locality, and Hua Hin in Prachuap Khiri Kahn. My four specimens are from the latter locality.

Remarks: Isopachys gyldenstolpei is a burrowing species with a cylindrical body. It has been found under logs. My specimens were found some inches underground in soft dry earth. Two, a male and a female, were taken together at the same time. The female contains five embryos.

When picked up the lizard usually remains very quiet with little or no movement, and no struggling to escape. The eye is not opened but I discerned some movement of the lower lid which seems to consist of a single scale. The five scales anteriormost on the upper jaw, and three on the lower, form a thickened cap. These presumably have developed in response to the burrowing habit. The color fades quickly in alcohol and the ground color becomes nearly ivory-white.

Associated with the pair (in the same area, two x two foot square) there were three specimens of *Ophioscincus anguinoides*, three

Typhlops braminus and two *Riopa bowringi*. A third specimen of *Isopachys gyldenstolpei* was found the following morning at the same place. Such a concentration of species has not been found heretofore. I could find no reason for this as there was no visible food supply, no especial cover such as logs or trash. However, the earth was dusty, soft, and offered little resistance in burrowing, and may formerly have been the site of a pile of rotting grass.

It seems to me that Lönnberg's genus *Isopachys* is distinct from other scincoid genera and should not be placed in the synonymy of *Ophioscincus*. It would appear that osteoderms in this genus differ from those in many skinks in that "the osteoderms are greatly thinned, so that they offer no obstacle to the passage of Röntgen-rays." This with the absence of prefrontals and frontonasal would seem to suffice to differentiate the genus from *Ophioscincus*. M. Smith calls attention to the condition of the palatine bones, originally described as separated, actually they are normally in contact and the apparent separation was due to a skull injury.

The species lives in loose soil where it burrows with ease.

FAMILY DIBAMIDAE Boulenger

Tongue short, bifid posteriorly, pointed, undivided in front, covered with curved lamellae and plicae. Teeth small, pointed, hooked, none on palate; no cranial arches; no infraorbital foramen; fore and hind limbs absent in female, the legs represented in male by a pair of flaps on each side of anal vent. Body vermiform covered with cycloid scales above and below; no osteoderms. Eyes concealed under the skin. No ear-opening; preanal pores one or two.

The family contains only one recognized genus, *Dibamus*. Some five or six forms have been described, and others now in various museums await description.

A single Thai species is known from Pattani province in southern Thailand.

Genus DIBAMUS Duméril and Bibron

Dibamus Duméril and Bibron, Erpétologie générale . . ., vol. 5, 1839, p. 833 (type of genus *Dibamus novae-guineae*).

Diagnosis: (See family characters); snout may be covered by a large rostral and a large labial on each side or these may be fused into a single shield; nostril in rostral with a straight horizontal suture behind it. Male with legs represented by two flaplike rudiments; no legs in female.

Dibamus alfredi Taylor

FIG. 99

Dibamus alfredi * Taylor, Univ. Kansas Sci. Bull., vol. 43, 1962, pp. 246-248, fig. 13 (type-locality, Na Pradoo, Pattani, southern Thailand).

Diagnosis: Snout subconical covered by a large rostral, with an entrant suture from ocular at about level of eye, extending forward but not reaching to level of nostril; frontal distinctly smaller than interparietal; 20 or 21 scalerows around body; four preanal pores in male, two in female. Transverse scalerows, 219-230.

Description of species (from type): Rostral large, rounded anteriorly, and in profile; nostrils lateral, pierced in rostral somewhat back of anteriormost point; snout projecting beyond mouth; posterior border of rostral emarginate; a small median frontal twice as wide as long, somewhat lens-shaped, bordered behind by a distinctly larger interparietal; latter bordered behind by five scales, shaped somewhat like regular body scales but distinctly larger; an ocular plate borders frontal and interparietal; eye covered by an ocular scale, but visible in outer anterior part of scale; a supralabial scale borders ocular laterally. Anterior to ocular at about level of eye an entrant suture in rostral extending forward, failing to reach as far forward as vertical level of nostril by a third of length of suture. A large infralabial on each side separated by a smaller trapezoidal mental.

Body scales smooth, subcycloid, or subhexagonal; 24 scalerows around back part of head; 22 on neck, 20 around middle of body, 20 preceding vent, and 20 around tail; tail rather short, blunt at tip, not ending in a spine. Legs flattened on ventral surface, which is covered with three scales at base followed by three pairs of scales and an elongate terminal scale; on dorsal surface, legs covered by about 18 scales; two preanal pores on each side; covered by a somewhat enlarged scale through which the two elongate pores are more or less visible. Triangular preanal area between folded limbs occupied by two transverse rows of three scales each, and an elongate terminal scale, its posterior half free. No ear-opening; eyes dimly visible through ocular.

Color in life: Generally violet to purplish brown, not or scarcely lighter below on ventral surfaces; underside of snout, a large area about nostril, sides of head, and anterior part of chin, cream to ivory-white. Preanal scales and dorsal surface of limbs white. On ventral surface of type, about 50 scattered ivory-white scales.

* Named for Mr. Eric Alfred of the Raffles Museum, Singapore.

FIG. 99.—*Dibamus alfredi* Taylor. No. 1385. Na Pradoo, Pattani, Thailand. Actual total length, 111.2 mm.

Measurements in mm. (Nos. 1386 ♀, 1385 ♂, 3174 ♂, and 3175 ♀, respectively): Snout to vent, 98, 94, 92, 99; tail, 15.6, 17.2, 17, 15; width of head, 3.1, 3.2, 3.2, 3.1; width of body, 4, 3.4, 3.7, 3.9; length of leg, —, 3, 3, —.

Variation: The female taken with the type agrees in most characters. The legs are absent. The ocular is bordered behind by two "postoculars"; 20 or 21 scalerows around middle of body, while there are but 18 around middle of tail. The male type has about 230 transverse scalerows; in this female there are 178 transverse scalerows on body, and 41 on tail, totaling 219; each of the two other specimens has 227 transverse rows; however, the body rows are 172 ♂ and 181, on the tails, 55 and 46.

At the base of the anal flap, there is a pair of large scales separated by a smaller scale; behind this is a transverse series of five scales followed by a transverse series of three bordering the vent. In the females I find only a single preanal pore present on each side. The ivory-colored scales on the venter are absent.

Distribution: B. M. No. 1903.4, 13.69, an egg containing a young specimen of a *Dibamus* discovered on Bukit Besar, Pattani, by Robinson (1903), and reported by Boulenger, is in the British Museum. I have examined this embryonic specimen but the scale sutures on the head are as yet not clearly discernible. It is to be presumed that it is the same species since the egg was found in the general vicinity where my adults were taken.

Tweedie, 1950, has reported a single specimen of *Dibamus* (as *novaeguineae*), 114 mm. long from Gua Madu, Gua Musang, Kelantan, Malaya, which may belong to this species.

Remarks: Dibamus alfredi seems to differ from a related species *Typhloscincus nicobaricus* Steindachner from the Nicobar Islands, as follows: there are 20 or 21 scalerows instead of "circa" 23; the entrant suture is, from the ocular; the rostral fails to reach the nostril (separated by one third of the length of the suture instead of entering the nostril); the rostral does not form a sharp angle posterolaterally, but is blunt; the labial scale is below (not behind) level of ocular; the interparietal is smaller and two small parietals on side of interparietal are not differentiated as shown in the Steindachner figure. (Novara Exped. Zool. Reptilien, Steindachner, pl. III, fig. 8 but not shown in fig. on p. 94).

The type of *Typhloscincus nicobaricus* could not be found at the Vienna Museum where it is presumed to have been deposited by Dr. Steindachner (*loc. cit.*) and the comparisons have been made with the type description and figures on plate 3, and figures on p. 94.

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